

ARTICLE



Patterns of genetic diversity and structure of a threatened palm species (*Euterpe edulis* Arecaceae) from the Brazilian Atlantic Forest

Aléxia Gonçalves Pereira ¹, Marcia Flores da Silva Ferreira ¹✉, Thamyres Cardoso da Silveira¹, José Henrique Soler-Guilhen¹, Guilherme Bravim Canal ¹, Luziane Brandão Alves ¹, Francine Alves Nogueira de Almeida ¹, Fernanda Amato Gaiotto ² and Adésio Ferreira¹

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The detection of distribution patterns of genetic diversity of plant and animal species has contributed to the understanding of biodiversity and evolutionary history of the Atlantic Forest. We used microsatellite markers to assess the genetic diversity and structure of 26 populations and 527 adult individuals of *Euterpe edulis*, a native palm which is an important food resource for fauna and is intensively exploited due to economic reasons. We found high genetic diversity and inbreeding in all populations analyzed. We report highest rates of inbreeding for this species, which could reflect the anthropic impacts of selective cutting, fragmentation, and change in foraging behavior from pollinators and less availability and mobility of large dispersers. We detected by STRUCTURE, two genetic groups, Northern and Southern, which divide the Brazilian Atlantic Forest geographically. These groups have low genetic admixtures, but we found a region of lineage hybridization in the contact zone with low recent gene flow. Distribution pattern of this species corroborates results from previous studies reporting the Last Glacial Maximum (LGM) have shaped the structuring of the species through movements of forests' expansion and contraction. The STRUCTURE analysis of each group revealed the presence of genetic subgroups with low rates of recurrent gene flow. Southern subgroups have higher rates of admixtures than the Northern subgroups, revealing greater historical connectivity of forests in this region.

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INTRODUCTION

The Atlantic Forest (Fig. 1) is the second-largest tropical forest in South America extending latitudinally from tropical to subtropical regions along the Brazilian coast, eastern Paraguay, and north-eastern Argentina (Joly et al. 1999; Oliveira-Filho and Fontes 2000; Ribeiro et al. 2009). Longitudinal extension provides the difference in forest composition and rainfall regime, such that on the coast where the forests are wetter and inland, where forests are drier (Câmara 2003). In addition, this biome has strong seasonality and environmental gradients connected to complex topography, making it exceptionally diverse and encompassing various types of vegetation (Fundação Instituto Brasileiro de Geografia e Estatística 1993).

Studies which analyzed Atlantic Forest species across geographic distribution reported latitudinal structure of genetic diversity and endemism in a north–south trend (Carnaval and Moritz 2008; Carnaval et al. 2009; Palma-Silva et al. 2009; d'Horta et al. 2011; Thomé et al. 2010; Aguiar-Melo et al. 2019; Turchetto-Zolet et al. 2013). The dynamics of the population's expansion and contraction due to climatic oscillations of the Last Glacial Maximum (LGM) may imprint a signal in the genetic species over time (Hewitt 2000; Gugger et al. 2013). Bottlenecks, genetic drift, and consequent loss of genetic diversity was expected in species during forest contraction (Pauls et al. 2013). During forest

expansion, it was expected an exchange of migrants between populations, promoting high genetic diversity which could increase genetic diversity per heterosis (Ortego et al. 2012). However, colonization of new habitats can result in loss of genetic diversity due to founder effects or due to the occurrence of outbreeding depression (Pauls et al. 2013; Collevatti et al. 2014).

The maintenance of biodiversity during the LGM's climate change took place through the green areas which remained climate stable. Three areas were identified in the Atlantic Forest, the Pernambuco and Bahia refuge to the north and the São Paulo refuge to the south (Carnaval et al. 2008; Carnaval et al. 2009). Palaeoclimatic evidence shows that climatic variability impacted the Northern and the Southern regions of the Atlantic Forest differently. The northern part was influenced by the drier conditions of the Eastern Amazon during the LGM, becoming more humid in the Middle Holocene (6 kay BP). The opposite occurred in the south of the Atlantic Forest, in the western Amazon, and in the Andes, so that the LGM was more humid and the Holocene drier (Cheng et al. 2013; Carnaval et al. 2014). This alternation may have promoted the genetic isolation of lineages and divergence over time, through genetic drift.

The distribution of the *Euterpe edulis* Martius palm (Arecaceae) in the Atlantic Forest of Brazil, Argentina, and Paraguay and in gallery forests of the Brazilian Cerrado (Henderson et al. 1995), was

¹Department of Agronomy, Universidade Federal do Espírito Santo, Alegre, Brazil. ²Department of Biological Sciences, Universidade Estadual de Santa Cruz, Ilhéus, Bahia, Brazil. Associate editor Thomas Meagher. ✉email: marcia.ferreira@ufes.br

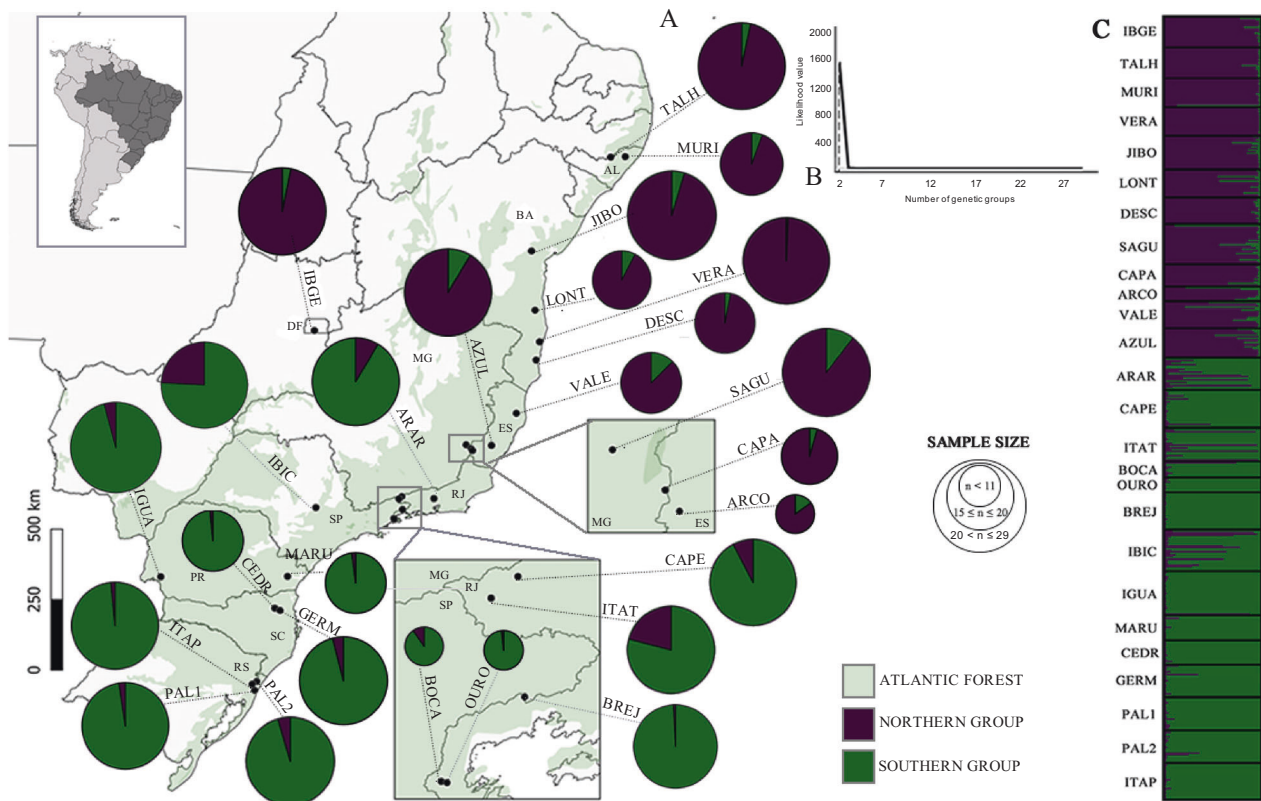


Fig. 1 Clustering analysis and geographical distribution of two geographic clusters in *Euterpe edulis*. **A** Geographical distribution in the Brazilian Atlantic Forest (light greenish-gray) and lineage assignments of populations to Northern group (dark purple) and Southern group (dark green). The diagram represents the average of each proportion of assignment (Q) of the genetic groups for the population contemporary gene pool. In light gray the map of Brazil, highlighting the region sampled in dark gray. **B** ΔK statistic, based on the likelihood function, identified $K = 2$ as the most appropriate number of genetic groups. **C** Graph of cluster analysis in STRUCTURE. Each horizontal bar represents an individual. The colors represent the coefficient of association for each genetic group (see Table 1 for population codes). AL Alagoas, BA Bahia, DF Distrito Federal, ES Espírito Santo, MG Minas Gerais, SP São Paulo, PR Paraná, SC Santa Catarina, and RS Rio Grande do Sul.

influenced by climatic events that have occurred since the LGM, mainly by the reduction of habitat suitability which occurred in the Holocene, restricting the species to the coast but preserving genetic diversity (Carvalho et al. 2017). Data obtained from fragmented and exploited areas show that young individuals and adults respond differently to human pressure, but the consequences of the exploitation process as an increase in inbreeding, decrease in diversity and genetic structuring, was not identified in the populations as expected (Santos et al. 2015; Gaiotto et al. 2003; Carvalho et al. 2016; Konzen and Martins 2017; Lauterjung et al. 2019). Many of the works developed with *E. edulis* cover restricted sampling areas, and for this reason, it is interesting to recognize possible distribution patterns of *E. edulis* genetic diversity throughout the biome.

The aim of this study consisted in evaluating the diversity and structuring of *E. edulis* along the Brazilian Atlantic Forest, to provide new insights about the genetic variability of this key species, which can drive sustainable strategies for conservation and use. We expected to find a high genetic diversity of *E. edulis* and detect latitudinal genetic diversity patterns throughout its distribution in the Brazilian Atlantic Forest.

MATERIALS AND METHODS

Study species

Euterpe edulis (Arecaceae) is a palm threatened with extinction, found in the Atlantic Forest of Brazil, Argentina, and Paraguay, and in gallery forests of the Brazilian Cerrado (Henderson et al. 1995). This species is widely distributed in the biome, occurring in different vegetation types within the Atlantic Forest, including Ombrophylous, Deciduous, and Restinga forests

(Henderson et al. 1995; Gatti et al. 2008), mainly associated with humid environments or close to watercourses (Galetti and Fernandez 1998).

The fruits of *E. edulis* are small and round (1 to 1.5 cm diameter), weighing about 1g. The seed constitutes 85% of the fruit and the mesocarp is fleshy and very thin, being an important food resource for birds and mammals (Bicudo et al. 2014; Galetti et al. 2013). During the ripening process, the color turns from green to black (Bicudo et al. 2014). Currently, the pulp extracted from ripe fruits is an income source for many smallholder communities due to its similarity to açai (Bourscheid 2011).

Euterpe edulis is a species of a single nonstoloniferous strain. It is monoic and pollinated by small *Trigona* bees (Reis and Kageyama 2000) having a low rate of self-pollination (Gaiotto et al. 2003). For many years this palm was known by the flavor of the edible meristem (heart of palm), much appreciated in cooking (Reis and Kageyama 2000). Target of intense exploitation since the 1960s, many populations of the species have been extinct locally or drastically reduced due to indiscriminate cutting (Fantini et al. 2000).

Sampling

We checked the occurrence and distribution of the species through Species Link (www.splink.org.br), Reflora (floradobrasil.jbrj.gov.br), and ICMBio (www.icmbio.gov.br) to select the sampling areas. We sampled 26 locations with natural populations of *Euterpe edulis*, 25 from the Brazilian Atlantic Forest Biome and one from the Cerrado Biome (Table 1 and Supplementary Material, Fig. S1). Samples ranged from 10 to 29 adult individuals from conserved vegetation areas, maintaining a distance of at least 5 meters between individuals. *Euterpe edulis* forms agglomerates of adult and young plants. We sought to sample different agglomerates from the same area to compose the samples. The population codes, localities, geographic coordinates, number of specimen, and references are shown in Table 1. The pairwise geographic distance (Km) among populations is shown in Table S1.

Table 1. *Euterpe edulis* populations and genetic diversity in nine microsatellite loci.

Population (code)	Locality	Latitude/Longitude	n	A _{priv}	A/locus	Ar	H _e	H _o	F	Q ₁	Q ₂
North group											
Reserva Ecológica do IBGE (IBGE)	Brasília, DF	-15.948141	20	5	7.1	4	0.8	0.5	0.1	1	0
Pedra Talhada (TALH)	Quebrangulo, AL	-9.244635	21	1	5.7	3	0.6	0.5	0.1	1	0
Estação ecológica de Murici (MURI)	Murici, AL	-9.22693	19	0	5.8	4	0.7	0.5	0.1	0.9	0.1
Estação de VERACEL (VERA)	Porto Seguro, BA	-16.387687	20	0	5.8	4	0.6	0.5	0.1	1	0
Serra da Jiboia Monte Cruzeiro (JIBO)	Elísio Medrado, BA	-12.872034	23	0	5.3	3	0.6	0.4	0.2	1	0.1
Parque Nacional da Serra das Lontras (LONT)	São José da Vitória, BA	-15.163974	18	0	6	4	0.7	0.5	0.1	0.9	0.1
Parque Nacional do Descobrimento (DESC)	Prado, BA	-17.93301	19	3	5.7	4	0.7	0.6	0.1	1	0
Parque Ecológico Sagui da Serra (SAGU)	Manhumirim, MG	-20.35629	26	3	9.4	5	0.8	0.6	0.1	0.9	0.1
Caparaó, Chalé dos Faria (CAPA)	Pedra Menina, ES	-20.503511	15	0	6.8	4	0.8	0.5	0.1	1	0.1
Cachoeira do Arco-íris (ARCO)	Patrimônio da Penha, ES	-20.580679	10	0	6	4	0.8	0.6	0.1	0.9	0.2
Reserva Natural da Vale (VALE)	Linhares, ES	-19.15131	19	5	7.6	4	0.8	0.4	0.3	0.9	0.1
Pedra Azul (AZUL)	Pedra Azul, ES	-20.38125	20	1	8.7	4	0.8	0.6	0.1	0.9	0.1
	North group average		230	18	6.7		0.7	0.5	0.1		
South group											
Reserva Biológica Estadual de Araras (ARAR)	Araras, RJ	-22.434722	21	1	8.1	5	0.8	0.6	0	0.3	0.7
Capelinha (CAPE)	Visconde de Mauá, RJ	-22.360278	25	0	7	4	0.8	0.7	0	0.1	0.9
Parque Nacional do Itatiaia (ITAT)	Itatiaia, RJ		23	0	7.6	5	0.8	0.6	0.1	0.2	0.8
Parque Nacional da Serra da Bocaina (BOCA)	Paraty-Cunha, RJ	-22.450029	11	0	4.7	4	0.7	0.5	0.1	0.1	0.9
Engenho D'ouro (OURO)	Paraty, RJ	-23.208423	10	0	5.3	4	0.7	0.6	0	0	1
Pousada Brejal (BREJ)	Bananal, SP	-23.213713	26	0	6	3	0.6	0.6	0.1	0	1
Estação ecológica de Ibicatu (IBIC)	Piracicaba, SP	-22.858592	28	0	7.9	4	0.7	0.5	0	0.2	0.8
Parque Nacional do Iguaçu (IGUA)	Foz do Iguaçu, PR	-22.782675	29	0	7	4	0.7	0.4	0.1	0	1
Parque Estadual Pico do Marumbi (MARU)	Morretes, PR	-25.461766	17	0	6.3	4	0.7	0.6	0	0	1
Rio do Cedros (CEDR)	Rio dos Cedros, SC	-25.445412	17	0	6.4	4	0.7	0.5	0	0	1
Parque Ecológico Freymund Germer (GERM)	Timbó, SC	-26.678569	21	0	8.8	4	0.8	0.6	0	0	1
Reserva Biológica da Mata Paludosa - Patch 1 (PAL1)	Itati, RS	-26.7643	23	0	7.2	4	0.7	0.5	0.1	0	1
Reserva Biológica da Mata Paludosa - Patch 2 (PAL2)	Itati, RS	-29.850833	22	1	7.3	4	0.8	0.6	0.1	0.1	1
Parque Estadual do Itapeva (ITAP)	Torres, RS	-29.51005	24	2	8.3	4	0.7	0.6	0.1	0	1
		-29.613333	297	4	7		0.7	0.6	0.1		
	South group average		297	4	7		0.7	0.6	0.1		
	Overall sum		527	22	-		-	-	-		
	Overall average				6.8		0.8	0.5	0.1		

The number of alleles (*n*), number of private alleles (*A_{priv}*), allelic richness (*Ar*), mean alleles per locus (*A/locus*), expected heterozygosity (*H_e*), observed heterozygosity (*H_o*), inbreeding coefficient (*F*), and proportion of assignment (*Q₁* = North group and *Q₂* = South group). Allelic richness (*Ar*) and expected heterozygosity (*H_e*) considering the differences in sample size among populations under analysis.

DNA extraction, microsatellite genotyping

We obtained the samples from the cortex of 527 adult individuals of *E. edulis*. Total genomic DNA was extracted according to a previously published protocol by Carvalho et al. (2019). The genotyping was performed using ten microsatellite markers dye-labeled for *E. edulis* published by Gaiotto et al. (2001) (see Table S2). These markers are codominant, highly variable, and widely used in the scientific community for work with *E. edulis* and species of the genus, which favors the comparison and interpretation of results. The selected microsatellite markers, the conditions for amplification and analysis of the fragments are displayed in Table S2.

We used one sample as a standard for fragment size. This sample was genotyped in all plates. When we detected changes in the standard's size, we corrected all other samples accordingly. We used this approach to avoid variation between different plates. Alleles were sized in an automated DNA sequencer (3500 Genetic Analyzer—Applied Biosystems) using GeneMarker software v.2.4 (Hulce et al. 2011) and LIZ 500 Size Standard (Applied Biosystems).

Data analysis—genetic diversity and population structure using molecular data

Initially, null allele frequencies for each *locus* were estimated using the Micro-Checker software version 2.2.3 (Van Oosterhout et al. 2004) with the Oosterhout algorithm. Subsequently, we used the FSTAT software, version 2.9.3.2 (Goudet 2002), to calculate the linkage disequilibrium between *loci* in all populations. The GDA software (Lewis and Zaykin 2002) was used to calculate the number of private alleles (A_{priv}), the number of alleles per locus ($A/locus$), and the observed heterozygosity (H_o). We also estimated the allelic richness (AR) and expected heterozygosity (H_e)—considering the differences in sample size among populations under analysis using the software FSTAT 2.9.3.2 (Goudet 2002). Finally, the software INEST 2.2 (Chybicki and Burczyk 2009) was used to estimate a corrected F accounting for the potential impacts of null alleles. This analysis was performed with the model based on a Bayesian approach (IIM), with 500,000 Markov chain Monte Carlo interactions and burn-in of 50,000.

The Mantel test was used to assess the correlation between geographical and genetic distances, as a predictor for isolation by distance (IBD). The pairwise Rousset's genetic distances $F_{ST}/(1-F_{ST})$ and the pairwise geographic distances (log transformed) of populations were carried out using the SPAGeDi (Hardy and Vekemans 2002). The correlation was evaluated using the Mantel test with 100,000 permutations, using the software R, package Vegan. Also, a clustering analysis was performed by the UPGMA method in the R software, using the pairwise Nei's standard distance among populations, which was estimated in the SPAGeDi.

To analyze *E. edulis*' genetic structure, we used the Bayesian approach of STRUCTURE 2.3.4 with admixture model (Pritchard et al. 2000) and frequency parameters of correlated alleles (Falush et al. 2003), with no prior information on the structure of the population. We used the parallelization of STRUCTURE executed in the program StrAuto (Chhatre and Emerson 2017) under Linux environment. This analysis allowed the smallest computational time. The run parameters were a burn-in period of 25,000 steps and 1,000,000 sampling steps with 20 independent repetitions of the Markov Monte Carlo Chain (MCMC) executions.

We allowed the model to analyze the probability of individuals belonging to different Bayesian groups (K ; the number of sampling sites plus 3, here $K = 29$) by analyzing the set of allele frequencies in each *locus* (Evanno et al. 2005; Pritchard et al. 2010). The best K was identified in Structure Harvester (Earl and VonHoldt 2011) using the ΔK method ($\Delta K = m(L''(K))/s(L(K))$; Evanno et al. 2005). The ΔK graph shows the distribution peak at the best value of K groups for the analyzed samples. These analyses allowed the detection of two distinct clusters with low admixture (see results). A separate STRUCTURE analysis was run with each of the genetic groups to identify subgroups. In these new analyses we considered $K = 15$ and $K = 17$. The CLUMPACK software (Kopelman et al. 2015) was used to align the 20 independent runs of STRUCTURE obtained for the best K value and to generate graphical outputs. For each population, we used the membership coefficients generated with CLUMPACK to obtain a diagram of the relative contribution of each lineage to the contemporary gene pool.

To assess whether stepwise mutations could have contributed significantly to genetic differentiation among populations or not, we applied an allele-size permutation test (Hardy et al. 2003) implemented in the SPAGeDi (Hardy and Vekemans 2002). This test compares the global R_{ST} values taking into account the allele sizes by stepwise mutations with a distribution of pR_{ST} values which consider allele identities by infinite allele model. If Global R_{ST} values >95% of the pR_{ST} indicates stepwise mutations

contributed to population differentiation and can be interpreted as presence of phylogeographical pattern (Hardy et al. 2003). We used 1000 allele-size permutations to run the test.

Partitioning of genetic variability within and among groups was tested by analysis of molecular variance (AMOVA) between the groups and subgroups derived from STRUCTURE, using ARLEQUIN v.3 (Excoffier et al. 2005). In ARLEQUIN, we also computed pairwise F_{ST} and R_{ST} of populations and tested the significance using 1000 permutations with 95% confidence intervals.

Contemporary gene flow rates (m) were assessed using the BAYESASS edition 3 software (Wilson and Rannala 2003), which estimates the proportion of migrants per generation over the past three generations. *E. edulis* requires about 10 years to reach its reproductive maturity (Leitman et al. 2013), and exhibits an overlapping of generations. Therefore, all estimates of gene flow must consider the past 30 years, and genetic processes after intensive habitat fragmentation and specie's exploitation in the study area. We used the genetic groups and subgroups detected by STRUCTURE to identify the clusters of populations. We carried out five independent simulations with random initial seeds following the recommendations of Chávez-Pesqueira and Núñez-Farfán (2016). Each run consisted of an MCMC of 10^8 iterations, sampled every 1000 iterations, with 10^7 iterations discarded as burn-in. The values of the MCMC admixture parameters for migration rates (gene flow), allele frequencies, and inbreeding coefficients were adjusted to achieve the recommended acceptance rates in the literature (Wilson and Rannala 2003). This procedure was repeated for each subcluster reported by STRUCTURE. The stationarity of the MCMC for each execution was confirmed using TRACER (Rambaut and Drummond 2007).

RESULTS

Genetic diversity and genetic differentiation

One of the 10 *loci* (EE52) exhibited null allele frequency above 0.2 and was discarded from all subsequent analyses. A total of 178 alleles were identified for the remaining nine *loci*; the number of alleles per *locus* ranged from 14 (EE9) to 24 (EE54) (Supplementary Material, Table S2). Pairwise comparisons among the 9 *loci* revealed no evidence of linkage disequilibrium. Observed and expected heterozygosity values per population ranged from 0.36 (JIBO and VALE) to 0.68 (CAPE) and from 0.54 (TALH) to 0.81 (ITAT), respectively, rendering mean values of 0.54 and 0.75. The values of inbreeding coefficient (F) were high in almost all populations, ranging from 0.03 (CAPE and IBIC) to 0.28 (VALE) with an overall mean of 0.07. Only nine of 26 populations had private alleles; TALH, AZUL, ARAR, and PAL2 (a single private allele per population); ITAP (two private alleles); DESC and SAGU (three private alleles per population); and IBGE and VALE (five private alleles per populations) (Table 1).

Regarding global R_{ST} , the average among all sample populations was significantly higher than the permuted value ($R_{ST} = 0.44$, $pR_{ST} = 0.19$, $P = 0.003$; Supplementary Material, Table S3). This suggests that stepwise mutations contributed to population differentiation in *E. edulis* and thus R_{ST} should be the estimator preferred over F_{ST} (Hardy et al. 2003). Pairwise R_{ST} values ranged from 0.03 (between IBIC and IGUA populations) to 0.81 (between VERA and OURO populations); all pairwise R_{ST} values were significant ($P < 0.05$), except for 16 pairs that displayed low population differentiation ($R_{ST} < 0.04$; Supplementary Material, Table S4).

Genetic structure

The Bayesian clustering analysis completed with the software STRUCTURE suggested two geographic groups (best $K = 2$, Fig. 1A, B) for *E. edulis*. The first one denominated the Northern group (depicted in purple; Fig. 1A, C) consisted of populations sampled in the north of the Brazilian Atlantic Forest (from Alagoas to Espírito Santo states), and the second group denominated the Southern group (depicted in green; Fig. 1A, C) consisted of populations sampled in the south of the Brazilian Atlantic Forest (from Rio de Janeiro to the Rio Grande do Sul states); the only population of *E. edulis* sampled in the Cerrado (IBGE population) was grouped in the Northern group (Fig. 1A, C). Most populations showed a proportion of

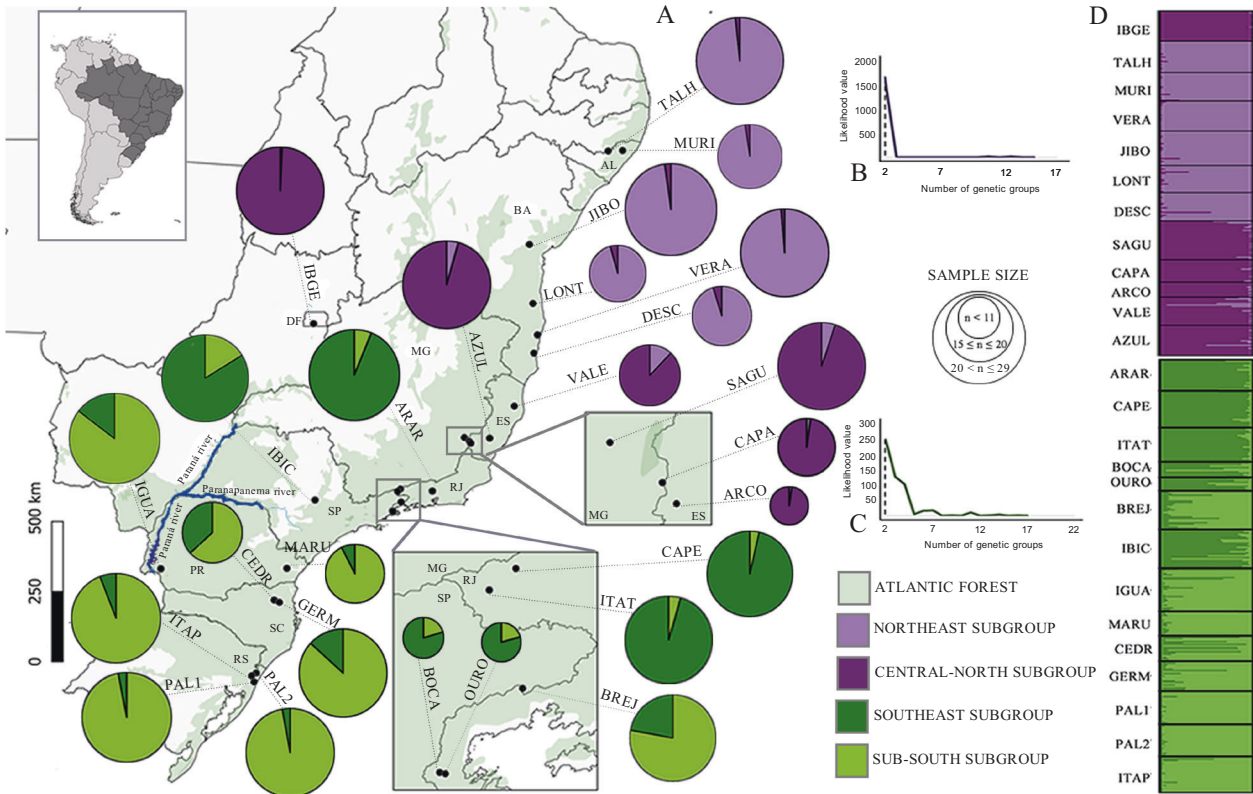


Fig. 2 Clustering analysis and geographical distribution of four geographic subgroups in *Euterpe edulis*. **A** Geographic distribution in the Brazilian Atlantic Forest (light greenish-gray) and lineage assignments of populations to Northeast subgroup (light purple), Central-North subgroup (purple), Southeast subgroup (green) and Sub-South subgroup (light green). The diagram represents the average of each proportion of assignment (Q) of the genetic groups for the population contemporary gene pool. In light gray the map of Brazil, highlighting the region sampled in dark gray. ΔK statistic, based on likelihood function, identified $K = 2$ for the Northern (**B**) and Southern (**C**) genetic group as the most appropriate number of genetic groups. The colors in purple tones represent the North group, and the colors in green tones represent the South group. **D** Graph of the cluster analysis in STRUCTURE. Each horizontal bar represents an individual. The colors indicate an association coefficient for each genetic subgroup (see Table 1 for population codes). The colors indicate an association coefficient for each genetic subgroup (see Table 1 for population codes). The rivers Paran and Paranapanema favor the maintenance of remnants of the Brazilian Atlantic Forest along its course and are possible limits for the distribution of contemporary plant lineages (Martins 2011). AL Alagoas, BA Bahia, DF Distrito Federal, ES Esprito Santo, MG Minas Gerais, SP So Paulo, PR Paran, SC Santa Catarina, and RS Rio Grande do Sul.

assignment over 90% to either cluster Northern or Southern (Table 1). In particular, the highest levels of admixture were detected in populations near the geographic contact between genetic groups, as the ARAR, ITAT populations from Rio de Janeiro state, and the ARCO and VALE populations from Esprito Santo state (Fig. 1A and Table 1).

The subsequent STRUCTURE analyses carried out separately for the Northern and the Southern groups are shown in Fig. 2. A value of $K = 2$ was found for both analyses (Fig. 2B, C, D). The populations within each group (Northern or Southern) were separated according to their geographic location, giving rise to the Northeast and the Central-Southeast subgroups as well as the Southeast and Sub-South subgroups (Fig. 2). The correlation between geographical and genetic distances was significant by the Mantel test (0.59 ; $P = 0.0001$), however the clustering pattern obtained in the STRUCTURE analysis was corroborated by UPGMA method (Fig. S2).

Contemporary migration rates were estimated as extremely low between groups (Northern and Southern) and between subgroups pairs (Northeast and the Central-Southeast; Southeast and Sub-South), with values of $m \leq 0.006$ in all comparisons (Fig. 3). Consequently, extremely high migration rates ($m > 0.99$) were observed within each group or subgroup (Fig. 3).

Hierarchical AMOVA showed that 26.74% of the genetic variation was explained by differences between Northern and Southern groups, with an R_{ST} value of 0.53; on the remaining variation, 26.60% was observed among populations within groups,

and 46.66% was within populations (Supplementary Material, Table S5). When AMOVA was evaluated within each group, Northern group had 33.03% of the genetic variation attributed to differences between Northeast and the Central-Southeast subgroups, while the Southern group had only 4.60% of the genetic variation attributed to differences between Southeast and Sub-South subgroups (Supplementary Material, Table S5). The genetic differentiation based on R_{ST} for the Northern subgroups and the Southern subgroups were of 0.58 and 0.15, respectively.

Overall, when populations of *E. edulis* were evaluated based on genetic groups, the mean genetic diversity was similar in both Northern and Southern groups (Table 1) and 37.64% of alleles are shared by both groups (Supplementary Material, Table S6). However, the Northern group had higher amounts of private alleles ($A_{priv} = 18$) compared to the Southern group ($A_{priv} = 4$). Analyzing the subgroups, the Center-Southeast has more private alleles ($A_{priv} = 14$) than the other subgroups and the Northeast has higher average alleles per locus ($A/locus = 11.70$; Central-Southeast, $A/locus = 7.60$; Southeast, $A/locus = 6.70$ and Sub-South, $A/locus = 7.16$) and a larger number of alleles considering all loci (Supplementary Material, Table S6).

DISCUSSION

In this study, we used microsatellite markers to evaluate the genetic diversity, and structure of the palm *E. edulis* along the Brazilian

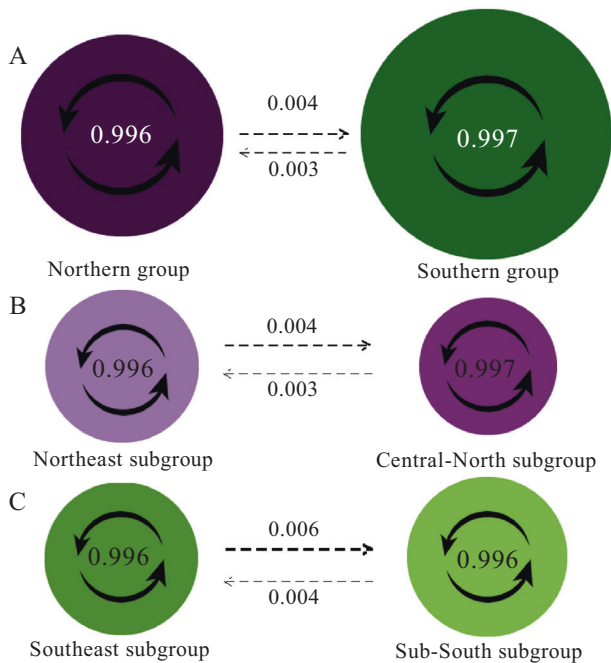


Fig. 3 Recurrent gene flow rates estimated by BayesAss analysis. **A** Rate of gene flow between the Northern (dark purple) and Southern (dark green) genetic groups. **B** Rate of gene flow between the Northeast (lilac) and Central-North (purple) genetic subgroups. **C** Rate of gene flow between the Southeast (green) and Sub-South (light green) genetic subgroups. The groups and subgroups analyzed were detected by population structure analysis using the STRUCTURE software. The circles correspond to each genetic group and subgroup and the size of the circles indicates the sample size (North groups with 230 individuals and south with 297 individuals; Northeast subgroups with 110 individuals, Central-North with 120 individuals, Southeast with 118 individuals and Sub-South with 179 individuals). The arrows inside the circle indicate the gene flow within the population and the horizontal arrows indicate the direction of gene flow between genetic groups and subgroups and their thickness varying with intensity.

Atlantic Forest. Our main results indicated: (1) high within-population genetic diversity and inbreeding coefficients (F range from 0.03 to 0.28); (2) the existence of phylogeographic pattern with two geographical genetic groups within the range of *E. edulis*, the Northern and Southern groups; (3) further subdivision of the Northern and Southern groups, the Northeast and Central-Southeast subgroups and the Southeast and Sub-South subgroups; and (4) limited genetic admixture between groups or subgroups.

High levels of genetic diversity and inbreeding of *Euterpe edulis*

The high levels of genetic diversity revealed in the *E. edulis* populations (mean $H_E = 0.75$; Table 1) is in accordance with previous studies on this species (Carvalho et al. 2015; Santos et al. 2015; Carvalho et al. 2017; Novello et al. 2017) and reinforces further the influence of the large historical effective size of *E. edulis* populations to the conservation of their current genetic diversity (Carvalho et al. 2015; Santos et al. 2015; Soares et al. 2019).

We detected inbreeding in all populations (Table 1), including relevant levels in Brazilian conservation areas as BOCA ($F = 0.14$) and ITAP ($F = 0.12$). The highest inbreeding value was found in the VALE population ($F = 0.28$), followed by JIBO ($F = 0.24$), both with a history of logging and further preservation. In populations with low density, the *Trigona spinipes* bee can keep inbreeding low by moving pollen between geographically more distant palm trees (800 m maximum flight distance) (Zurbuchen et al. 2010; Côrtes

et al. 2013; Carvalho et al. 2017). However, reestablishing the high density of population, some intercrossing among kinship could contribute to the increase of inbreeding generation after generation (Ghazoul 2005; Carvalho et al. 2017). Furthermore, there is a positive relationship between the density of mother plants and the number of dispersed seeds, promoting greater dispersion of related genotypes (Carvalho et al. 2021).

Two genetic lineages in the Brazilian Atlantic Forest revealed by Microsatellite markers

We show that *E. edulis* has two genetic lines, to the North and South of the Brazilian Atlantic Forest ($R_{ST} = 0.53$). A large number of private alleles in the Northern group ($A_{priv} = 18$, Table 1) and the low levels of admixture observed between the genetic groups are indicative of long-time isolation of population, low historical gene flow, and differentiation by genetic drift. Similar values of genetic diversity between the Northern and Southern groups (Table 1) show the maintenance of genetic heterogeneity along the Atlantic Forest.

The analysis carried out within each genetic group showed the structuration of subgroups, with isolation after the differentiation of the Northern and Southern groups. The differentiation between the subgroups has similar intensity to the differentiation observed in the groups, due to the low genetic mixture between them (Fig. 2) and high $R_{ST} = 0.58$ (Table S5). We did not identify an increase in values of genetic diversity or private alleles in populations in the Northeast subgroup, as expected for areas next to refuges of Bahia and Pernambuco (Carnaval et al. 2009). However, we found a larger number of different alleles, suggesting the persistence of the species in this area (Petit et al. 2002). The high rate of private alleles in the IBGE and VALE populations (five each, Table 1) suggests small *E. edulis* refuges in the states of Espírito Santo state and Distrito Federal (Central-North subgroup). These regions showed habitat suitability throughout the LGM climate change as detected by Carvalho et al. (2017).

We found less differentiation between Southern subgroups (percentage variation = 4.6), higher mixing ratios between subgroup lineages, and a low number of private alleles ($A_{priv} = 4$, Table 1) as expected in areas with shorter isolation time (Szpiecha and Rosenberga 2011). This suggests that Southern subgroups come from a more recent structuring process than the subgroups of the Northern Group.

The current low gene flow between the groups and the subgroups (Fig. 3) arises possibly due to Atlantic Forest fragmentation, loss of large frugivores, and greater difficulties in seed movement (Carvalho et al. 2015; Carvalho et al. 2016; Carvalho et al. 2021) between populations. Thus, the genetic exchanges of groups and subgroups reflect conditions that are much older than those predicted by the gene flow analysis (Fig. 3).

The Southeast and Sub-South subgroups of *E. edulis* showed a limit of division between the states of São Paulo and Paraná. This delimitation is in accordance with the distribution limits of habitat suitability in different climatic cycles (Carvalho et al. 2017). Some features of this region are identified as isolating factors for some species, such as the plateau in the state of Paraná (Cortez et al. 2019), the Paraná and Paranapanema rivers (Martins 2011) and the transition between tropical and subtropical forests due to difference in annual precipitation and soil types (Cabanne et al. 2007; Cabanne et al. 2008; Thomé et al. 2010; d'Horta et al. 2011).

The diversity and endemism, Northern and Southern oriented, is a phylogeographic pattern already reported for other species in the Brazilian Atlantic Forest (Martins et al. 2007; Carnaval et al. 2014; Costa et al. 2017). Carnaval et al. (2014) relate this to the influence of different climatic regimes during the Last Glacial Maximum (LGM = 21 kyr PB). The climatic fluctuation in the Quaternary helps to understand the suitability of habitat for *E. edulis* during the LGM. Our hypothesis is that these cycles of retraction and expansion may have led to the differentiation of the Northern and Southern groups of *E. edulis*, due to the loss of genetic variability and differentiation of

populations during retractions and hybridization in contact zones of different groups during expansions.

The habitat suitability analysis for *E. edulis* showed that the Brazilian Atlantic Forest coast has remained stable throughout climate change and may represent refuge for the species (Carvalho et al. 2017). Phylogeography studies can help to understand the distribution of *E. edulis* genetic diversity through the dating of the divergence of the Northern and Southern groups and testing our hypothesis. The evolutionary history of the southern part of the Brazilian Atlantic Forest is complex and involves several processes (Martins 2011). Therefore, our study with *E. edulis* clearly provided useful information to help the understanding of the evolution of the southern part of the Brazilian Atlantic Forest.

The identification of different genetic lineages, in the Northern and Southern regions of the Brazilian Atlantic Forest, shows that it is necessary to increase the sampling effort in restoration projects to obtain seeds that contribute to the remaining gene pool of different geographic regions. Our work showed the importance of conservation areas for the preservation of *E. edulis*. Therefore, we support the creation of new units like the proposal for the Recôncavo Sul Baiano (Blengini et al. 2015) that includes the JIBO population. Struggling with illegal palm heart cutting is a challenge, mainly due to the difficulties of monitoring large conserved areas. We reinforce the importance of support and investment in inspection, as well as the use of the species in forest restoration projects.

DATA AVAILABILITY

Microsatellite genotypes and geographic location of samples are available from the Agri-Environmental Research Data Repository at the University of Guelph (<https://doi.org/10.5683/SP2/KRHVEH>).

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AUTHOR CONTRIBUTIONS

AGP designed research, data analysis and wrote the paper. TCS data analysis and wrote the paper. JHS-G and GBC coordinated sampling. LBA and FN helped with performed molecular biology. FAG assistance with microsatellite genotyping and wrote the paper. MFSF conception and design of the project, secured funding and wrote the paper. AF conception and design of the project, data analysis, secured funding and wrote the paper.

COMPETING INTERESTS

The authors declare no competing interests.

ADDITIONAL INFORMATION

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Correspondence and requests for materials should be addressed to Marcia Flores da Silva Ferreira.

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