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RESEARCH

Genetic diversity of the endangered palm *Butia eriospatha* in grassland and forest landscapes: informing conservation and seed collection

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Abstract

The Atlantic Forest is a biodiversity hotspot facing severe habitat loss and fragmentation, with most of its remnants experiencing biomass and biodiversity declines. *Butia eriospatha*, an endangered palm species endemic to this biome, is threatened with extinction by habitat loss, poaching, and lack of regeneration. Despite its ecological and cultural importance, genetic studies have focused only on open grassland populations, leaving the rare forest populations unexplored. Here, we compared genetic diversity aspects of a forest (FOR) and a grassland (GRA) *B. eriospatha* population to inform seed collection guidelines and further expand our knowledge on the genetic conservation of this important species. Using nine microsatellite loci, we assessed genetic diversity, mating system, and spatial genetic structure (SGS) of both populations. We found that both FOR and GRA had moderate genetic diversity but were significantly differentiated from each other, despite the short geographic distance. Allogamy predominated in both populations, with a small proportion of mating among relatives detected in the forest population. SGS was weak but extended over longer distances in FOR (up to 60 m) compared to GRA (up to 30 m), suggesting differences in mortality dynamics. To maximize genetic diversity in long-term conservation strategies, seeds should be collected from 132 to 139 seed-trees, respecting SGS distances. Our findings highlight the need to conserve both grassland and forest populations to safeguard *B. eriospatha*'s genetic diversity.

Keywords Endangered species · Fine-scale spatial genetic structure · Arecaceae · Mating system · Genetic diversity

Introduction

The Atlantic Forest is one of the most diverse biomes on Earth with high levels of endemism, and yet, it has been one of the most fragmented and threatened ecosystems over the past centuries (Joly et al. 2014). Recent estimates suggest that only 28% of this biome remains in some preserved form (MapBiomas Project 2025), within one of the most populated regions in South America (de Lima et al. 2024). Habitat reduction drives biodiversity loss not only at the taxonomic level (Newbold et al. 2015), but also at the intraspecific level (Exposito-Alonso et al. 2022), further jeopardizing the maintenance of species and their ecological interactions, particularly under climate change scenarios (Calambás-Trochez et al. 2021; Marchioro et al. 2023). It is estimated that more than 80% of the remaining fragments in the Atlantic Forest suffer from biomass and biodiversity losses, what reduces their conservation value (de Lima et al. 2020). Furthermore, 65% of all tree species in this biome were recently classified as threatened (de Lima et al. 2024). Therefore, there is an urgent need and a congruent opportunity for better conserving and ecologically restoring the Atlantic Forest (Brancalion et al. 2019).

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Despite the long-known importance of the maintenance of genetic diversity to safeguard the adaptive potential of endangered species in conservation and restoration programs (Jordan et al. 2019; Thomas et al. 2014), only recently this recognition has translated into practical recommendations and international policies in an attempt to safeguard minimum levels of genetic diversity within natural ecosystems (Hoban et al. 2021, 2023). Studies explicitly testing the effects of genetic diversity of source and sampled populations of trees on the success of restored tropical and subtropical forest ecosystems, more than just diversity of species, are still lacking but recent theoretical and empirical work has supported the importance of adequate genetic diversity for maintaining the adaptive potential in other groups of organisms (Kardos et al. 2021). Better understanding the levels of intraspecific genetic variation is critical to inform management of endangered tree species (Hoban et al. 2021). This involves identifying unrelated individuals within and among genetically diverse populations for proper seed sourcing, and potentially taking into consideration different aspects of local adaptation and climate change for deployment of seedlings (Aitken et al. 2024; Jordan et al. 2024). Guidelines with recommended number and distance between sampled seed-trees, as well as number of seeds to be collected from each seed-tree, are crucial and may vary among species, but are still largely insufficient for endangered Atlantic Forest tree species (but see Conceição et al. 2024; Costa et al. 2021; Montagna et al. 2019; Rodrigues et al. 2023).

One of the goals in conservation genetic studies is to investigate to what extent anthropogenic changes of natural ecosystems have affected the genetic composition and evolutionary trajectories of natural populations, and to provide genetic-based guidelines for restoration and conservation efforts, enhancing the chances of success in such actions. One way to approach this in trees is to compare populations from "less disturbed" sites with populations from "more disturbed" sites regarding multiple genetic parameters. Studies in this context have assessed the effects of habitat loss and fragmentation on the genetic composition of species by testing for genetic differences between populations within different levels of forest cover (e.g., Browne et al. 2015; Da Silva Carvalho et al. 2015; Santos et al. 2015; Zechini et al. 2018). However, for some palm species, after disturbance, individuals may occupy environments that do not correspond to a forest fragmentation gradient, with entire populations occurring in disturbed open grasslands (e.g., *Butia eriospatha*; Candido-Ribeiro et al. 2019). Comparisons regarding genetic diversity between forested and disturbed open grassland habitats are, therefore, necessary to inform further conservation and restoration actions for some endangered palm species in the Atlantic Forest.

Palm trees are key organisms, exceptionally relevant for maintaining their communities (Andreazzi et al. 2009; Galetti et al. 1999) and sustaining intimate relationships between human societies and their natural ecosystems (Johnson 1988; Macía et al. 2011), especially in the Neotropics (Andrade et al. 2024; Muscarella et al. 2020). Restoration programs in tropical and subtropical regions should prioritize native palms species, given their capacity to facilitate the re-establishment of multiple ecological interactions and functions of depauperate communities on degraded environments (Reis et al. 1999). Given the ecological importance and unique cultural value of *B. eriospatha* in the highlands of southern Brazil (Sosinski et al. 2019; Wagner et al. 2025), and yet its worsening conservation status in the past decades, the need for restoration and conservation strategies for this species has become urgent. Illegal poaching of centenary individuals (Nazareno and Reis 2014a), habitat loss and fragmentation, changes in seed morphology and reproductive patterns likely related to habitat changes (Candido-Ribeiro et al. 2019), and cattle grazing resulting in lack of regeneration by new recruitments (Nazareno & Reis, 2014b), are some of the major threats populations of *B. eriospatha* face. *Butia eriospatha* is currently listed as "Endangered" on the IUCN Red List (Amorim and Heiden 2025), but official regional lists classify this species as under high risk of extinction (CONSEMA-SC, 2014; SEMA-RS, 2014).

Despite being described as a grassland species (Reitz 1974), *B. eriospatha* populations, formed almost exclusively of adult individuals, have also been observed in forested landscapes (Candido-Ribeiro et al. 2019), and in current grassland areas that were covered by forest in the past (>60 years ago) (Candido-Ribeiro 2017). Yet, it is not clear what the species' preferred habitat is, nor what role it plays in the forest succession dynamics where it occurs. The current knowledge on the genetic conservation status of *B. eriospatha* is based solely on studies of grassland populations (Nazareno & Reis, 2014b; Reis et al. 2012), while forest populations have not been genetically characterized. In a study that described phenotypic and demographic differences between a forested and a grassland *B. eriospatha* population, Candido-Ribeiro et al. (2019) observed that, despite the higher density of adult *B. eriospatha* individuals observed in the forest landscape, a much lower proportion of individuals tends to reproduce within a season in this environment when compared to the nearby open grassland. This raises questions of whether the effective population size of a forested population could be reduced, increasing potential genetic drift, reducing genetic diversity, and rising the risks associated with inbreeding depression in following generations. On the other hand, the forest environment could give more opportunities for more diverse interactions

with pollinators than a disturbed open grassland landscape. This could increase outcrossing rates, optimize dispersal, and reduce risks associated with inbreeding in the population. In fact, Candido-Ribeiro et al. (2019) observed significantly larger seeds in the forested population, potentially suggesting higher fitness than in the grassland population. Therefore, the potential differences in genetic diversity between these two contrasting habitats could be of key importance for the establishment of optimal conservation and seed sourcing strategies.

In this study, expanding on Candido-Ribeiro et al. (2019) work on *B. eriospatha*, we tested the following hypotheses: (a) a given forested population should present higher outcrossing rates, and lower levels of fine scale spatial genetic structure among the reproductive individuals within the population when compared to an adjacent grassland population. (b) No genetic differentiation in the cohort of adults should be expected between two populations occupying these two contrasting environments and separated by only 2 km, but a significant differentiation is expected in the cohort of seedlings. (c) Lower genetic diversity would be observed in the seed cohort of both populations than in the adult populations. Finally, (d) we tested the hypothesis of complete spatial randomness in the distribution of adult individuals in the grassland and forested populations. Here, we present a comprehensive description of the genetic diversity, mating system, and fine-scale spatial genetic structure in two populations of *B. eriospatha* occurring in two contrasting environments, open grassland and forest. We also provide seed collection guidelines to inform restoration and conservation efforts for this important palm species.

Methods

Study area and sampling design

In 2015, we established two nearly square five-hectare plots on a private property (−27°12′1″; −50°36′31″) in the state of Santa Catarina, southern Brazil, to investigate the two contrasting environments where the palm *B. eriospatha* occurs (Fig. 1). One plot is in an open grassland environment (GRA), typical of open Araucaria Forest stands where the most economically valuable tree species were harvested

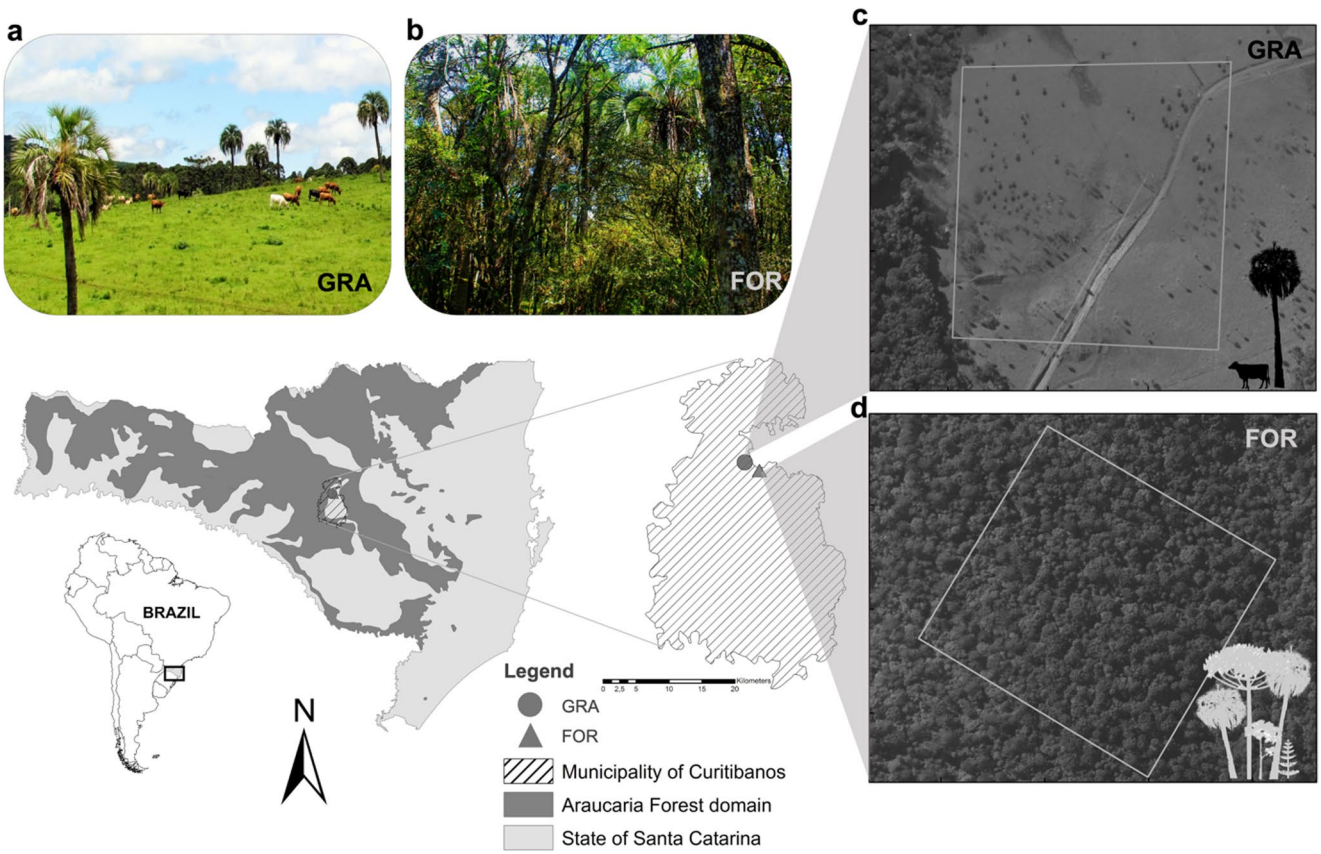

Fig. 1 Studied *Butia eriospatha* populations, GRA (open grassland in **a** and **c**) and FOR (forest in **b** and **d**), where the nearly square plots of c. 5 ha each were established (grey squares within each population in c and d). The two populations are located in Curitibanos, SC, Brazil. Aerial photos WMS were obtained from the Santa Catarina's geographic information system at http://sigsc.sc.gov.br/sigserver/SIGSC/wms. Photo credits in **a**: Juliano Zago da Silva; and in **b**: Rafael Candido-Ribeiro

for timber production and the area has been designated for cattle grazing for more than 60 years (Fig. 1). Adult individuals of *B. eriospatha* are the only arborescent plants left and maintained in this area, likely due to the economic importance of their fronds in the recent past, and the past and current appreciation for their fruits (amongst other reasons described in Candido-Ribeiro et al. (2019). Cattle is constantly grazing in this area and from time to time the area is also mowed or burned. GRA has a total density of 19.1 individuals ha^{-1}, with 92% being reproductive (Fig. 2d). The average height and diameter of individuals in GRA is 5.65 m and 31.92 cm respectively (Candido-Ribeiro et al. 2019).

The second plot (FOR) is located in a remnant of Araucaria Forest with *B. eriospatha* individuals co-occurring underneath the canopy of other remarkable tree species of this biome, such as *Araucaria angustifolia* and *Podocarpus lambertii*. The FOR area was systematically managed in the past for timber supply but was never transformed into an open grassland environment and only low-impact selective logging was practiced (Fig. 1). GRA and FOR are approximately 2 km apart. The density of individuals in FOR is 43.2 individuals ha^{-1}, with only 28% reproductive (Fig. 2a). The average height and diameter of individuals in FOR is 5.78 m and 33.37 cm respectively (Candido-Ribeiro et al. 2019).

Both plots were further subdivided into 400 m^2 subplots (20 × 20 m) to facilitate the identification of the relative position of individuals in a Cartesian plane (XY coordinates; Fig. 2a, d). In 2015, all *B. eriospatha* individuals were identified, given their XY position within each plot, and classified according to the ontogenetic classes proposed by Nazareno & Reis, (2014b). We sampled leaflets from all adult individuals within the demarcated plots for DNA extraction and genotyping (209 individuals in FOR and 109 in GRA). A more detailed description of the plots and the region can be found in (Candido-Ribeiro et al. 2019).

As only a few regenerating seedlings of *B. eriospatha* were found in FOR and none was found in GRA, likely due to cattle herbivory (Nazareno & Reis, 2014b), we collected c. 39 seeds on average per seed-tree from 18 randomly selected individuals in FOR and 16 in GRA to represent the next generation of the two populations. The only field criterion used to select the seed-trees was the presence of ripe fruits during multiple seed collection campaigns between February and March 2016. We germinated the seeds in controlled conditions for subsequent genotyping and estimation of genetic parameters of the seed cohort and mating system.

DNA extraction and genotyping

We performed nuclear DNA extraction from fresh leaflets of sampled adults and seedlings following the protocol described by (Doyle and Doyle 1990) with some modifications.

Genotyping was done with ten microsatellite markers (SSR) – seven markers were developed by Nazareno et al. (2011), and three were developed by the authors to increase the number of polymorphic sites (Table S1. Supp. Mat. 1). The seven markers developed by Nazareno et al. (2011) have been successfully used for the estimation of genetic parameters in other populations of *B. eriospatha* (Nazareno and Reis, 2012, 2014a, 2014b), despite their apparent low polymorphism. In order to optimize the genotyping and assist the identification of alleles, we used two multiplex assays. One with five pairs of primers that amplified the microsatellite regions at an annealing temperature of 54° C, and the other with five pairs of primers with annealing temperature of 56° C. The forward sequence of each SSR primer was marked with a fluorochrome (FAM, PET, NED, and VIC). To avoid overlapping of bands marked with the same fluorescence pattern, the same fluorochromes were used only for distant markers based on the number of amplified base pairs.

The SSR regions were amplified via Polymerase Chain Reaction (PCR) with a reaction solution of 10 μl in each well of the 96-well plates. The reaction solution consisted of 5 μM of KAPA 2G Fast Multiplex PCR Kit (Kapa Biosystems), 0.04 μM to 0.11 μM of one of the multiplex assays, and 2 μM of the sample (pure DNA of an individual). The final volume was completed with Milli-Q water. For the PCR cycles, we used the protocol described by Kapa Biosystem: 3 min at 95° C for the initial denaturation, 30 cycles of 15 s at 95° C for the denaturation, 30 s at the specified temperature of each multiplex for the annealing, 60 s at 72° C for the extension, and at the end of 30 cycles, 60 s at 72 ° C for the final extension. PCR amplifications were performed with a VERITI 96-Well thermocycler, 0.2 ml (Applied Biosystems).

In a new 96-well plate, we mixed 1 μM of diluted (1:20) amplified reaction solution, 8.75 μM of Formamide Hi-Di, and 0.25 μM of GS600 LIZ Size Standard (Thermo Fisher). The genotypes were identified by capillary electrophoresis in the ABI 3500xl−24 capillary sequencer (Applied Biosystem) and the allele frequencies for each analyzed locus were verified and interpreted with GeneMapper v.4.1 (Applied Biosystem).

Due to genotyping errors, 12 adult samples from FOR and 5 from GRA were discarded to avoid inaccurate genetic estimates (Costa et al. 2019), totaling 197 and 104 genotyped adult individuals, respectively. Due to failures in germination and genotyping, it was only possible to obtain the genotypes from 1 to 14 seedlings per reproductive individual. In total, 121 and 122 seedlings from FOR and GRA respectively were genotyped.

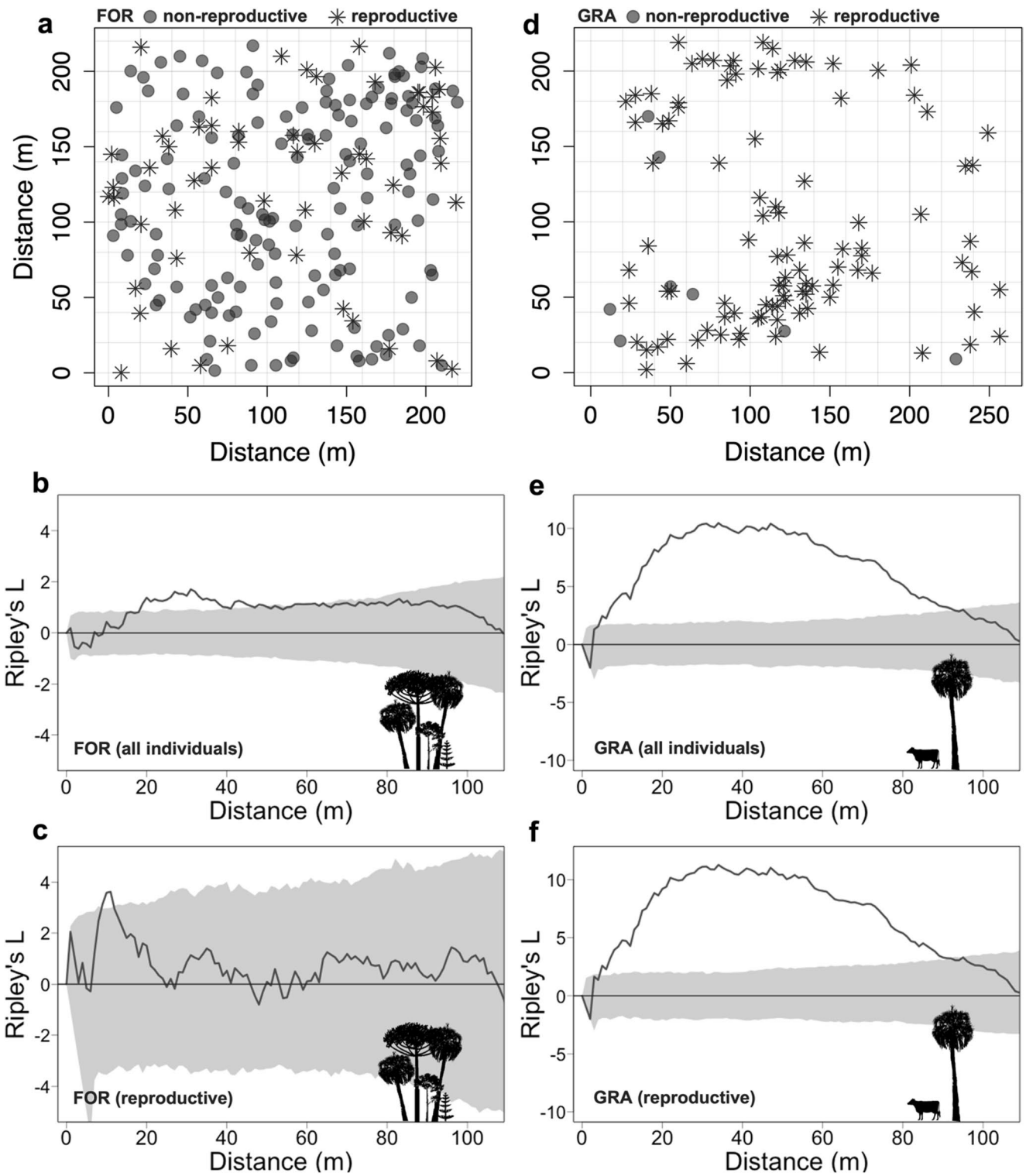

Fig. 2 Spatial distribution pattern in the two *Butia eriospatha* populations represented by the Ripley's K transformed (L). Map of non-reproductive and reproductive individuals identified within the FOR population ($n=151$ and 58, respectively) (**a**), and within the GRA population ($n=8$ and 101, respectively) (**d**). Spatial distribution pattern of all individuals in the forest population (FOR) (**b**), and in the open grassland population (GRA) (**e**), and only of reproductive individuals in FOR (**c**), and GRA (**f**). Gray ribbons depict the 95% confidence intervals after 1,000 Monte Carlo simulations. Complete randomness is given by an overlap between the black line the confidence interval

Analyses

Spatial distribution pattern

We tested the hypothesis of complete spatial randomness of all individuals and of only reproductive individuals in each plot (GRA and FOR), by applying the Ripley's K function (Ripley 1977). For this analysis, we used the package "spatstat" v. 1.45–2.45(Baddeley et al. 2016) in R – v. 4.0 (R Core Team 2021), with a Ripley's isotropic function for edge effect correction (Ripley 1977). To determine whether the observed spatial pattern differed significantly from complete spatial randomness, we obtained 95% confidence intervals after 1,000 Monte Carlo simulations. The maximum distance analyzed by the function corresponds to half the size of the smallest plot side (110 m). To improve the visual interpretation of the results, we transformed the Ripley's K function to the Ripley's L function. Direct comparisons were made to verify whether the two sampled plots differed regarding the spatial pattern distributions of individuals and at what distances such differences occurred.

Genetic diversity

First, we checked for the presence of null alleles with Microchecker - v.2.2.3 (Van Oosterhout et al. 2004), and linkage disequilibrium (LD) with FSTAT v.2.9.3.2 (Goudet 1995). All loci were also tested for Hardy-Weinberg equilibrium by the hypothesis of heterozygous deficiency, applying the exact test (Guo and Thompson 1992) implemented in Genepop v.4.6 (Rousset 2008).

After performing pairwise tests among all ten loci for linkage disequilibrium (LD), all were found to segregate independently, with the exception of locus *B.eri07*, which showed significant LD in relation to locus *B.eri15* in the adult populations ($p < 0.01$) and to locus *but23* in the progeny populations ($p < 0.001$), after Bonferroni correction for multiple comparisons. Therefore, locus *B.eri07* was excluded from all subsequent analyses, resulting in nine microsatellite loci used to determine genetic diversity, structure, mating system, and spatial genetic structure of both *B. eriospatha* populations. To validate the discriminatory power of our markers, we performed an exclusion probability (i.e., identity) test with the nine microsatellite loci in CERVUS (v. 3.0.7; Kalinowski et al. 2007). We observed an exclusion probability of 0.999955, indicating high confidence in the capacity of our markers to discriminate individuals within and between populations and to estimate genetic diversity.

From the allele frequencies obtained for all SSR loci in both populations and generations within populations, we estimated the following genetic parameters: total number of alleles, average number of alleles per locus ($\widehat{A}$), allelic richness ($\widehat{A}_R$), effective number of alleles per locus ($\widehat{A}_e$), number of exclusive alleles ($\widehat{A}_P$), number of rare alleles ($\widehat{R}$, allele frequency < 0.05), observed heterozygosity ($\widehat{H}_o$), and expected heterozygosity under Hardy-Weinberg Equilibrium ($\widehat{H}_e$). We also estimated the intrapopulation fixation index ($\widehat{f}$), and fixation index between populations ($\widehat{F}_{ST}$; (Weir and Cockerham 1984). The effective population size ($\widehat{N}_e$) was estimated as proposed by Li (1976).

Total number of alleles, $\widehat{A}$, $\widehat{A}_e$, $\widehat{A}_P$, and $\widehat{R}$ were estimated in GenAlEx 6.503 (Peakall and Smouse 2012). Before comparing the two populations for $\widehat{A}_R$, we standardized the number of alleles to the smallest sample size by applying the rarefaction method and bootstrapping (10.000) in R - v 4.0 (R Core Team 2021). We used FSTAT 2.9.3.2 (Goudet 1995) to estimate $\widehat{H}_o$ and $\widehat{H}_e$ and the PopGenKit R package (Paquette 2012) to calculate 95% confidence intervals (CI) based on 1.000 bootstrap resamples among individuals for both parameters. We used FSTAT 2.9.3.2 (Goudet 1995) to estimate $\widehat{F}_{IS}$, $\widehat{F}_{ST}$, and the 95% CIs. CI (95%) for $\widehat{f}$ was carried out in GDA (Lewis and Zaykin 2002) using 1.000 bootstrap resamples over loci, excluding one population at a time. To test for differences between populations and generations within populations regarding their genetic diversity, we made direct comparisons between group confidence intervals (i.e., an overlap means that there is no significant difference).

We used two additional approaches to infer the genetic structure between and within FOR and GRA populations. Both analyses were performed in the LEA package (v 3.8.0, Frichot and François 2015). First, individual admixture coefficients were estimated from the genotypic matrix with a sparse non-negative matrix factorization function (*snmf*) (Frichot and François 2015). Second, we used Principal Component Analysis (PCA) for the same genotypic matrix and plotted the first two PCs to qualitatively assess the level of genetic differentiation between the two populations. Given the geographic proximity of the two sites and our goal was to test the hypothesis of a single population, we restricted the admixture analysis for $K = 1$ and $K = 2$. The most likely number of genetic groups (i.e., either one or two genetic groups) was determined based on the minimum cross-entropy score.

Mating system

Only reproductive individuals (i.e., families) with a minimum of six genotyped seedlings were considered for the

estimation of mating system parameters. Allele frequencies for six to 12 seedlings from each of the 14 reproductive individuals (115 seedlings in total) in FOR, and for seven to 14 seedlings from each of the 12 reproductive individuals (116 seedlings in total) in GRA were used.

We used the mixed mating model (Kermit Ritland and Jain 1981) and the correlated mating model (Ritland 1989) implemented in the software MLTR 3.4 (Kermit Ritland 2009). The parameters estimated at the population level were multi-locus outcrossing rate ($\widehat{t}_m$), single-locus outcrossing rate ($\widehat{t}_s$), rate of selfing ($\widehat{s} = 1 - \widehat{t}_m$); selfing plus mating among relatives ($1 - \widehat{t}_s$). mating among relatives ($\widehat{t}_m - \widehat{t}_s$), multi-locus correlation of paternity ($\widehat{r}_{p(m)}$), inbreeding coefficient of maternal parents ($\widehat{F}_m$), proportion of half-sibs ($\widehat{P}_{hs}$), proportion of full-sibs ($\widehat{P}_{fs}$), proportion of self-sibs ($\widehat{P}_{ss}$), coancestry coefficient within progeny ($\widehat{\theta}_{xy}$; (Sousa et al. 2005), effective size of the variance ($\widehat{N}_{e(v)}$; (Cockerham 1969), and estimated number of seed-trees necessary to form a population with an effective population size of 500 after seed collection ($\widehat{m}_{(500)}$) for medium to long-term conservation of genetic diversity within populations (i.e., > 50 generations) (Alexandre Magno Sebbenn 2002). We tested for significance and difference between populations for each parameter using confidence intervals (95% probability) constructed from 1.000 bootstrap resamples among families. From the results on paternity correlation, the effective number of pollen donors (N_{ep}) was also estimated ($N_{ep} = 1/\widehat{r}_p$).

Fine-scale spatial genetic structure

To determine the fine-scale spatial genetic structure (SGS) within both FOR and GRA populations, we used all genotyped and mapped adult individuals described above. Multilocus pairwise comparisons among individuals within eight distance classes (K = 8. from 0 to 200 m) were performed to determine the average coancestry (i.e., Nason's kinship coefficient, $\widehat{F}_{ij}$) (Loiselle et al. 1995) within each class. The statistical significance calculated for each distance class was tested using confidence intervals, built from 10.000 permutations of individuals between different distance classes. This analysis was performed with the program SPAGeDi v. 1.4 (Hardy and Vekemans 2002). For a better comparison between the two populations, and for comparisons with other populations or species, we also calculated the $\widehat{S}_p$ statistic as in Vekemans and Hardy (2004). Neighbourhood size ($\widehat{N}_b$; Vekemans and Hardy 2004) and deme size for reproductive individuals within each population were estimated as described in Montagna et al. (2018).

Results

Spatial distribution pattern

When considering all individuals present in the population (n = 209), FOR presented a predominantly random spatial pattern. Between 0 and 20 m, a random pattern was observed, becoming aggregated between 20 and 45 m, and random between 45 and 110 m (Fig. 2a). When looking only at reproductive individuals (n = 58), we observed that FOR maintained the predominant random pattern of spatial distribution, with a small exception between 9 m and 11 m (Fig. 2b). Therefore, individuals in the FOR population did not differ significantly from the hypothesized Complete Spatial Randomness (CSR) for most of the analyzed distances. The GRA population presented a predominantly aggregated spatial distribution pattern when all individuals were considered (n = 109). A random pattern was observed between 0 and 5 m, and between 90 and 110 m. Between 5 and 90 m, the distribution pattern was aggregated (Fig. 2c). When only reproductive individuals were considered (n = 101), the observed spatial distribution pattern was almost identical to the observed for the whole population (Fig. 2d). Therefore, the spatial distribution pattern observed in GRA differs significantly from the hypothesized CSR within most of the analyzed distances.

Genetic diversity and structure

In total, we sampled and genotyped 544 *B. eriospatha* individuals, 301 of which were adults and 243 were progenies. All the information regarding allele frequencies obtained for the nine microsatellite loci used, as well as the sample size obtained for each locus in both populations are shown in Table S1, Supp. Mat. 1. Across all adult individuals and progeny in FOR and GRA populations, 42 alleles were observed, and the *but07* locus showed the largest number of alleles, with nine in total (Table S1. Supp. Mat. 1). The loci *B.eri15*, *but17* and *but23* presented only two alleles each (Table S1. Supp. Mat. 1).

Both FOR and GRA populations showed deviations from Hardy Weinberg equilibrium (HWE) in the class of adults and progenies (p < 0.001). Specifically, within FOR, the loci *B.eri11*, *but07*, and *but09* for adults and *B.eri11*, *but07*, and *but23* for progenies showed deviations from HWE. Within GRA, the loci *B.eri11* and *but07* for adults, and *B.eri11*, *but07*, and *but08* for progenies were not in HWE. These deviations were, to some extent, likely caused by the presence of null alleles at loci *B.eri11* and *but07* in both adult and progeny cohorts, and at locus *but23* in the progeny cohort for both populations. These loci were, nevertheless, maintained given the already reduced number of polymorphic loci in our study.

Within the FOR population, 32 alleles were detected in the adults and 29 in the progeny. Within GRA, we detected 31 alleles in the adults and 32 alleles in the progeny. All loci were polymorphic in adults and progeny in both populations, with two to seven alleles per locus in FOR, and two to eight alleles per locus in GRA. On average, the number of alleles per locus ($\widehat{A}$) within each studied group ranged from 3.2 (FOR progenies) to 3.6 (FOR adults and GRA progenies). The average number of alleles per locus for the cohort of adults in the GRA population was 3.4 (Table 1).

The number of alleles found in the cohort of adults in FOR was not significantly different from GRA ($\widehat{A}_R$ = 3.3; *p-value*>0.05). In the progeny, even after rarefaction correction, the allelic richness in GRA was higher than the observed in FOR ($\widehat{A}_R$ = 3.4 in GRA, and $\widehat{A}_R$ = 3.1 in FOR, *p-value* < 0.05) (Table 1). The progeny in GRA showed a number of effective alleles ($\widehat{A}_e$) of 2.25, and in FOR, 2.03. The adult cohort in GRA and FOR presented 2.15 and 2.08 effective alleles, respectively. Five exclusive alleles ($\widehat{A}_p$) were observed in adults within FOR, and four within GRA. Three exclusive alleles were observed in the progeny in FOR, and six in GRA. Eight rare alleles ($\widehat{R}$) were observed in the adults, and five in the progeny of both populations.

We did not detect a significant difference between GRA and FOR adult's observed heterozygosity ($\widehat{H}_o$, 0.447 and 0.440, respectively), nor expected heterozygosity ($\widehat{H}_e$, 0.445 and 0.441, respectively) (Table 1). In the progeny, no significant difference was observed between the two populations for $\widehat{H}_o$ and $\widehat{H}_e$, with 0.400 and 0.442 in GRA, and 0.357 and 0.429 in FOR respectively (Table 1).

The fixation index ($\widehat{f}$) in the adult and progeny cohorts did not differ significantly from zero in both populations (Table 1), indicating no deviation from Hardy-Weinberg equilibrium, on average (i.e., across all loci). Due to the low rate of fixation observed, the effective population size ($\widehat{N}_e$) in adults did not differ from the sample size (n) in both populations. For the progeny, $\widehat{N}_e$ was slightly smaller than n in both populations ($\widehat{N}_e$ = 104 in FOR and 111 in GRA, Table 1). A significant genetic differentiation between the two populations was observed, with an estimated $\widehat{F}_{ST}$ of c. 0.02 for the adult population and c. 0.03 for the progeny (p<0.05, Table 1).

The structure analysis revealed two most likely genetic groups – Group 1 (dark gray) and Group 2 (light gray) (Fig. 3), with populations FOR and GRA presenting different proportions of each genetic group across adult and progeny cohorts. Among adult individuals in FOR, 66% of the ancestry was represented by genetic Group 1 and 34% by Group 2, while among the progeny, 19% and 81%, respectively (Fig. 3a). Among GRA adult individuals, 81% of the population is represented by Group 1, and 19% by Group 2, while among the progeny, 52% and 48%, respectively.

Table 1 Genetic diversity descriptors for adult and seedling cohorts in the two studied ***Butia eriospatha*** populations (FOR and GRA)

Populations	n	Number of alleles	$\widehat{A}$	$\widehat{A}_R$	$\widehat{A}_e$	$\widehat{A}_p$	$\widehat{R}$	$\widehat{H}_o$	$\widehat{H}_e$	$\widehat{f}$	$\widehat{N}_e$	$\widehat{F}_{ST}$
Adult												
FOR	197	32	3.6	3.3[a]	2.08	5	8	0.440 (0.417–0.465)	0.441 (0.423–0.455)	0.002[ns]	197	0.019*
GRA	104	31	3.4	3.3[a]	2.15	4	8	0.447 (0.422–0.472)	0.445 (0.422–0.458)	−0.004[ns]	104	
Progeny												
FOR	121	29	3.2	3.1[b]	2.03	3	5	0.357 (0.334–0.381)	0.429 (0.409–0.439)	0.167[ns]	104	0.029*
GRA	122	32	3.6	3.4[a]	2.25	6	5	0.400 (0.377–0.425)	0.442 (0.424–0.454)	0.097[ns]	111	

n: sample size; $\widehat{A}$: number of alleles per locus; $\widehat{A}_R$: allelic richness after rarefaction; $\widehat{A}_e$: effective number of alleles per locus; $\widehat{A}_p$: number of exclusive alleles; $\widehat{R}$: number of rare alleles; $\widehat{H}_o$**(95% CI)**: observed heterozygosity (95% confidence interval); $\widehat{H}_e$**(95% CI)**: expected heterozygosity (95% confidence interval); $\widehat{f}$: fixation index; $\widehat{N}_e$: effective population size; $\widehat{F}_{ST}$: fixation index due to population subdivision

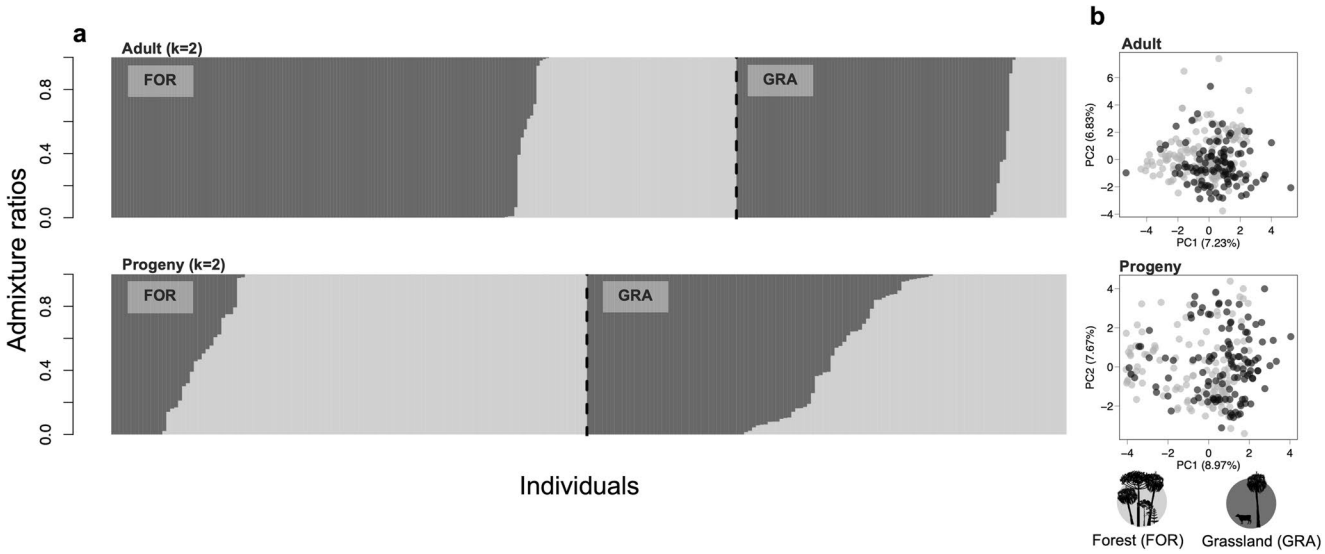

Fig. 3 Population structure in the *Butia eriospatha* FOR (forest) and GRA (open grassland) populations. **a** Admixture plots estimated for $K=2$. **b** PCA plots. Both Analyses were performed in the LEA package (v 3.8.0, Frichot and François 2015). Groups 1 and 2 in (a) are represented by the dark gray and light gray colors, respectively. Each bar in (a) represents an individual, and the dashed black line separates populations FOR and GRA. Percentages in brackets in the x and y axes in (b) depict the proportion of the total variance explained by the first two PCs

A non-parametrical Wilcoxon rank-sum test revealed that the genetic Group 2 was significantly more abundant in FOR among adult individuals ($W=11{,}810$; *p-value*$=0.0079$), and among the progeny ($W=10{,}739$; *p-value*<0.001) than in GRA. Despite differences in the proportion of genetic groups in each population, the PCA did not show any clear separation between FOR and GRA individuals regardless of cohort (Fig. 3b). These PCA results contrast with the low but significant levels of genetic differentiation observed between populations, in particular for the progeny cohort (Table 1).

Mating system

The multi-locus outcrossing rate ($\widehat{t}_m$) did not differ significantly from one (1.0) in both FOR and GRA populations ($\widehat{t}_{m\,FOR} = 0.865$; $\widehat{t}_{m\,GRA} = 0.930$) indicating that selfing is unlikely to happen within these two populations (Table 2). However, not all observed crossings in the FOR populations were among non-relatives, indicated by the $\widehat{t}_s$ (single-locus crossing rate) significantly different from the unit (0.848). In the GRA population, $\widehat{t}_s$ was not significantly different from one (Table 2). The proportion of the progeny generated by a single father ($\widehat{r}_{p(m)}$) and the inbreeding coefficient of maternal parents ($\widehat{F}_m$), were not significantly different from zero in both populations. FOR showed a proportion 71% of half-siblings ($\widehat{P}_{hs}$), and GRA, 81% (Table 2). The coancestry observed within progeny ($\widehat{\theta}_{xy}$) in both populations, was not significantly different from 0.125, i.e., the expected coancestry among half-siblings. It would be necessary a number of 139 and 132 seed-trees in FOR and GRA populations respectively to create populations with an effective population size (N_e) of 500 (Table 2), and 28 and 26 seed-trees respectively if the goal were populations with an N_e of 100.

Fine-scale spatial genetic structure

We observed significant levels of coancestry among individuals within a radius of up to 60 m in FOR and up to 30 m in GRA (Fig. 4). The maximum level of coancestry was observed for individuals up to 15 m apart ($\widehat{F}_{ij}=0.038$ in FOR; $\widehat{F}_{ij}=0.051$ in GRA). No coancestry was observed when only reproductive individuals were considered in FOR. In GRA, the spatial genetic structure remained unchanged with only reproductive individuals. The neighborhood size ($\widehat{N}_b$) estimated for reproductive individuals in GRA was 237, and in FOR, 260. Deme sizes based on the density of reproductive individuals in each population were 13 ha and 21.6 ha in GRA and FOR, respectively. The $\widehat{S}_p$ statistic found for GRA was 0.00507 for all individuals and 0.00421 for only reproductive individuals; in FOR, the $\widehat{S}_p$ statistic was 0.01196 for all individuals and −0.00385 for only reproductive individuals. The larger $\widehat{S}_p$ statistic observed in FOR among all individuals reflects the stronger SGS in FOR (Fig. 4), but the negative value detected among reproductive individuals indicates that reproductive individuals are reasonably geographically and genetically separated.

Table 2 Mating system estimates for both forest (FOR) and grassland (GRA) *Butia eriospatha* populations

	Population [95% CI]*			
	FOR		GRA	
Number of sampled trees (number of progeny)		14 (115)		12 (116)
Multi-locus outcrossing rate: $\widehat{t}_m$	0.865	[0.631–1.009]	0.930	[0.858–1.010]
Single-locus outcrossing rate: $\widehat{t}_s$	0.848	[0.568–0.996]	0.935	[0.838–1.014]
Selfing rate: $1-\widehat{t}_m$	0.135	[0.000–0.369.000.369]	0.070	[0.000–0.142.000.142]
Selfing+mating among relatives: $1-\widehat{t}_s$	0.152	[0.004–0.432]	0.065	[0.000–0.162.000.162]
Mating among relatives: $\widehat{t}_m-\widehat{t}_s$	0.017	[0.000–0.097.000.097]	−0.005	[0.000–0.045.000.045]
Multi-locus correlation of paternity: $\widehat{r}_{p(m)}$	0.052	[0.000–0.124.000.124]	0.059	[0.000–0.104.000.104]
Inbreeding coefficient of maternal parents: $\widehat{F}_m$	0.060	[−0.200-0.158]	−0.036	[−0.200-0.084]
Proportion of half-siblings (%): $\widehat{P}_{hs}$	70.93	[39.44–97.82]	81.39	[71.81–100.0]
Proportion of full-siblings (%): $\widehat{P}_{fs}$	3.890	[0.000–9.187.000.187]	5.103	[0.000–9.431.000.431]
Proportion of self-siblings (%): $\widehat{P}_{ss}$	1.800	[0.000–13.60.000.60]	0.500	[0.000–2.100.000.100]
Coancestry coefficient within progeny: $\widehat{\theta}_{xy}$	0.139	[0.117–0.150]	0.132	[0.118–0.141]
Variance effective size: $\widehat{N}_{e(v)}$	3.592	[3.204–4.000.204.000]	3.783	[3.543–4.000.543.000]
Number of seed-trees for a $\widehat{N}_e$ of 500: $\widehat{m}_{(500)}$	139	[116–156]	132	[118–141]
Number of seed-trees for a $\widehat{N}_e$ of 100: $\widehat{m}_{(100)}$	28	[25–31]	26	[25–28]
Number of seed-trees for a $\widehat{N}_e$ of 50: $\widehat{m}_{(50)}$	14	[12–16]	13	[12–14]

*Confidence interval estimated from 1.000 bootstrap resampling

Discussion

Establishing seed collection criteria for endangered tree species aimed at restoration and conservation programs (e.g., minimum number of seed trees and the distances among them) is critical to safeguard the long-term maintenance of genetic diversity in these species. Nevertheless, the lack of basic information about the genetic status of populations for many tree species in the tropics and subtropics is still a barrier for such actions. Here we provided a detailed description of the genetic diversity, mating system, and fine-scale spatial genetic structure in two populations of *Butia eriospatha*–occurring in open grassland and forest habitats–to inform seed collection efforts for the genetic conservation of this remarkable and endangered palm species.

To the best of our knowledge, our study represents the first description of genetic diversity in a *B. eriospatha* population occurring within a forest environment. Overall, we found high outcrossing rates and similar, moderate levels of genetic diversity in both the grassland and forest populations; however, important differences were observed despite their proximity (c. 2 km). Specifically, we detected significant genetic differentiation between the two populations, characterized by distinct proportions of the two identified genetic groups (i.e., groups identified with the structure analysis). A more marked fine-scale spatial genetic structure was observed within the forest environment, where related individuals spanned larger areas. However, no internal structure was observed when only reproductive individuals were considered. On the other hand, reproductive individuals in the open grassland population showed significant levels of spatial genetic structure. Allogamy was predominant in both populations, with a small proportion of crosses among relatives detected in the forest environment.

Differences between populations

The open grassland population (GRA) was spatially more aggregated than the forest population (FOR) for the analyzed scale range. The site where GRA is located has been subjected to more intense interventions in the past decades (e.g., cattle presence, mowing, fire, and more accessible to fruit collectors), despite the maintenance of the adult *B. eriospatha* individuals. These more stressful conditions can increase mortality rates, maintaining groups in more favorable micro-environments. When mortality occurs due to abiotic factors, there is a tendency for individuals to occur in more suitable habitat patches where resources are less limited (Hutchings 1997). This can promote a negative density-dependence relationship, increasing the aggregation of individuals. Other species-specific factors, such as reproduction and dispersal regime (Silva et al. 2012),

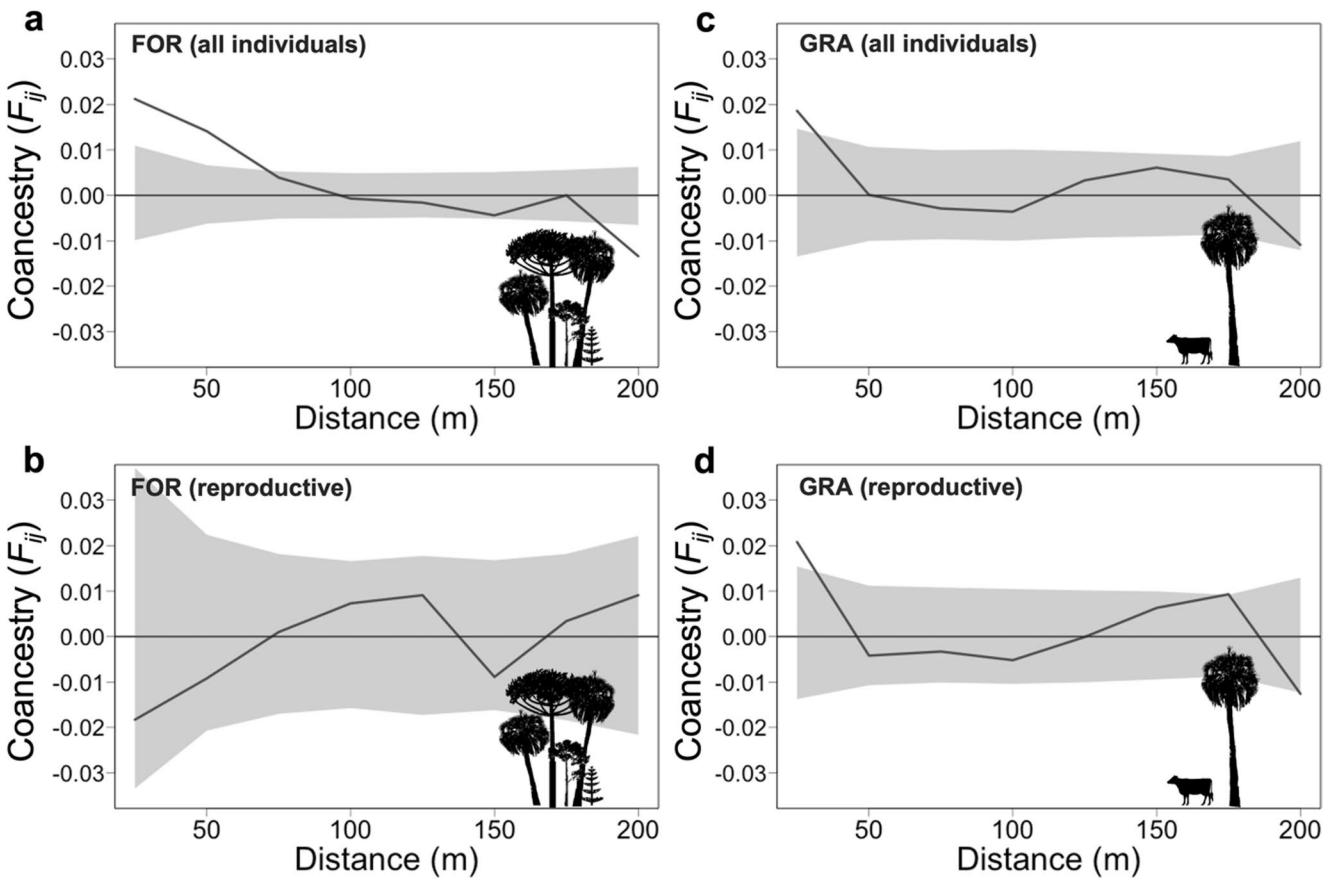

Fig. 4 Correlograms of coancestry (F_{ij}) for pairs of *Butia eriospatha* individuals. **a** All individuals in the forest population (FOR). **b** Reproductive individuals only in FOR. **c** All individuals in the open grass land population (GRA). **d** Reproductive individuals only in GRA. Ribbons depict 95% confidence intervals around zero (no kinship)

can contribute to the spatial distribution of trees (Willson 1993). No inferences about the spatial distribution pattern of lower age classes in both populations was possible given that no seedlings or saplings were observed in GRA, and only a handful of seedlings were found in FOR. The lack of continuity of generations in the two sites, makes it difficult to fully understand the potential causes and effects of the spatial pattern observed among adults, and also suggests an imminent collapse of these two populations.

In general, the assessed microsatellite loci presented low polymorphism, ranging between 2 and 8 alleles per locus, with allelic richness varying between 3.2 and 3.6. An average of 4.4 alleles per locus was previously observed among four *B. eriospatha* grassland populations (Nazareno & Reis, 2014b). Low allelic richness has also been reported for other palm species studied with microsatellites (Rodríguez-Peña et al. 2014), however, some species may exhibit moderate, e.g., *Oenocarpus batua* (6.5 alleles per locus) (Ottewell et al. 2012), or high allelic richness, e.g., *Euterpe edulis* (9.2 alleles per locus) (Da Silva Carvalho et al. 2015). When comparing the two populations, allelic richness, and the number of effective alleles in GRA was higher than in FOR (Table 1), and the number of exclusive alleles in the progeny of GRA was double ($\widehat{A}_p$ = 6) the number observed in the progeny of FOR ($\widehat{A}_p$ = 3). These differences suggest that open grassland areas are more likely to promote gene flow than forested areas and are also more prone to gene flow with pollen originating from outside the population, which maintains slightly higher levels of genetic diversity. A distinct pollination regime between the two environments could help explain these findings. While forest environments are expected to harbor higher levels of arthropod diversity (Seibold et al. 2019)–the primary group contributing to the pollination of the genus *Butia* (Mourelle et al. 2016; Perdomo et al. 2024)–the greater light exposure in the grassland environment likely promotes increased flowering, more effective pollination, and consequently higher seed production (Candido-Ribeiro et al. 2019), as observed in other palm species (Romulo et al. 2022).

In both populations, observed heterozygosity was close to the expected heterozygosity in adult individuals. This resulted in non-significantly different from zero fixation indices ($\widehat{f}$), indicating that, in both populations, the probability of two alleles being identical by descent at a locus

within the same individual is close to zero (Allendorf et al. 2022). Despite the slight increase in $\hat{f}$ for the progeny, these values were still not significantly different from zero, indicating that genetic diversity could be maintained in these two populations if a new generation was able to get established. Contrasting with these results, other studies reported significant $\hat{f}$ values for several *B. eriospatha* populations. For example, (Nazareno and Reis 2014a) found that six out of eight sampled natural populations showed significant $\hat{f}$ values. Another study with 14 populations found substantial variation for this parameter, but six populations presented high and significant $\hat{f}$ (Reis et al. 2012). This suggests that while some *B. eriospatha* populations have been able to maintain genetic diversity–such as the two populations analyzed here–others may have already experienced considerable losses.

We observed a significant genetic differentiation ($\widehat{F}_{ST}$) between the GRA and FOR for both adult and progeny cohorts, suggesting that even short distances (e.g., 2 km) can produce a certain degree of historical and current reproductive isolation between *B. eriospatha* populations. This may be associated with the pollen and seed dispersal regime of the species, carried out by small insects and animals that travel short distances. Long-distance pollen dispersal could prevent genetic isolation, allowing the cross-pollinating population to extend beyond its geographic limits (Cottrell et al. 2009). Nevertheless, the increased structuring in the progeny observed in this study may indicate a deficiency of these vectors in the landscapes where *B. eriospatha* occurs. Strong and significant $\widehat{F}_{ST}$ has been previously observed among more distant *B. eriospatha* populations in the state of Santa Catarina (Nazareno and Reis 2014a; Reis et al. 2012). This indicates that a large proportion of the genetic variation in the species is likely maintained among populations. Over time, genetic structuring can lead to fixation and loss of alleles, increasing homozygosity and reducing genetic diversity within populations (Hartl and Clark 1997). In fact, GRA and FOR presented alleles that were not present in the two populations used in the primer note to describe seven of the nine loci used here (Nazareno et al. 2011), nor in other nine populations analyzed by (Nazareno and Reis 2014a), which also used these same seven microsatellite loci.

We confirmed the predominance of allogamy in *B. eriospatha* for the assessed reproductive event in both GRA and FOR population. Similar outcrossing rates have been observed in other palm species, such as *Euterpe edulis* (Seoane et al. 2005), *Astrocaryum aculeatum* (Ramos et al. 2011), *Oenocarpus batua* (Ottewell et al. 2012), and *Acrocomia aculeata* (Lanes et al. 2016). Likewise, a similar result was observed by (Nazareno & Reis, 2012) in another grassland *B. eriospatha* population in Santa Catarina state, albeit a small significant deviation from unity ($\widehat{t}_m$= 0.961). Many tropical tree species have mechanisms to prevent self-fertilization and mating among related individuals (Degen and Sebbenn 2016). *Butia eriospatha*, for example, despite being monoecious, exhibits protandrous inflorescences (Nazareno & Reis, 2012), what prevents pollen from male flowers fertilizing female flowers on the same individual. Despite this, Nazareno & Reis (2012) results suggest that self-fertilization can also be present in the species. The wide confidence interval for the multi-locus outcrossing rate ($\widehat{t}_m$) observed in FOR (Table 2), may be associated with a large variation in this parameter among seed-trees.

The single-locus outcrossing rate ($\widehat{t}_s$) was not significantly different from the unity in GRA, indicating that all sampled seeds in the population derived from crosses between unrelated individuals, and reinforcing that gene flow is likely more efficient in GRA. In FOR, on the other hand, the estimated $\widehat{t}_s$ suggests that although there were no signs of self-fertilization, a small portion of the sampled seeds were generated from inbreed crosses. Although this level of $\widehat{t}_s$ in FOR was not enough to make the fixation index in the progeny significant (Table 1), it indicates a certain deficiency in gene flow and contradicts our initial expectation of higher outcrossing rates in the forested population. In addition, the estimated number of fathers per mother plant indicates that about 9% of the reproductive population in FOR contributed to the formation of the seeds of each mother plant, while this proportion reached 15% in GRA. Outcrossing levels should be further investigated in other forested populations, and the main pollinators in forested and grassland *B. eriospatha* populations should be described in order to confirm and potentially explain these patterns.

Fine-scale spatial genetic structure (SGS), formed due to clustering of related individuals within populations of trees, can lead to inbred crosses (Sebbenn 2006). Some differences were observed between GRA and FOR regarding SGS among adult individuals. The maximum coancestry in FOR was observed at a distance scale of up to 15 m ($\widehat{F}_{ij}$= 0.038). This is less than the expected between first-degree cousins (0.0625). Therefore, up to a distance scale of 15 m, the probability of two randomly sampled alleles in two adult individuals being identical by descent in the population is less than 4%. At the same distance scale (15 m), coancestry in GRA reached a higher value ($\widehat{F}_{ij}$ = 0.051). When considering all individuals present in FOR, family structure was detected up to a scale of approximately 60 m, despite being of low intensity. In GRA, coancestry was detected up to 30 m of distance between individuals. However, when only the reproductive individuals were considered, coancestry ceased to be significantly different from zero at any distance in FOR, but not in GRA. This suggests that a possible alternation of reproductive individuals at each reproductive

event in forest *B. eriospatha* populations (Candido-Ribeiro et al. 2019) could help reduce inbred crosses, but the reduced number of individuals participating in one reproductive event still produces inbred offspring, as suggested by the single-locus outcrossing rate observed in this population (Table 2). On the other hand, a more effective gene flow and the larger number of reproductive individuals in GRA seems to offset the stronger coancestry observed at shorter distance scales in this population, maintaining diversity in the progeny.

A potential explanation for the overall weak SGS observed within both GRA and FOR is the described demographic pattern of both populations, currently composed of only adult senescent individuals (Candido-Ribeiro et al. 2019). Mortality of senescent individuals, despite representing a loss of alleles due to genetic drift, tends to decrease family structure within populations. Studies that analyzed SGS at different ontogenetic stages within tropical palm populations detected a reduction in family structure as individuals advanced through demographic classes, precisely due to mortality in the populations (Browne et al. 2015; Choo et al. 2012). Therefore, it is likely that in *B. eriospatha* populations like these, seed dispersal, so important in determining the family structure of palm populations (Choo et al. 2012), gradually lost its importance as a determining factor in the distribution of genetic variation, and mortality of adult individuals has become the main factor shaping SGS in both GRA and FOR populations.

Implications for conservation and recommendations for seed collection

GRA and FOR populations exhibited considerable levels of genetic diversity with non-significant fixation indexes, making them suitable for seed collection for conservation, restoration, or the establishment of breeding populations. The absence of strong differences in genetic diversity levels indicates that collections could be conducted in either population. However, the presence of exclusive alleles in the progenies ($\widehat{A}_p$ = 3 and 6 for FOR and GRA, respectively), along with detectable genetic divergence ($\widehat{F}_{ST}$ = 3%), suggests that greater genetic diversity would be contemplated if seed collections were conducted in both populations. Selfing is unlikely to be happening in these two populations, which is important for avoiding the rapid rise of inbreeding in the progeny. However, inbreeding can also arise from crosses among related individuals. This was observed in FOR but it was not sufficient to generate a significant fixation index. In general, gene flow has been efficient in promoting random crosses within each population. Yet, in order to generate a new population with an effective population size ($\widehat{N}_e$) of 500, seeds would have to be collected from 132 to 139 seed trees in GRA and FOR, respectively. If the two studied populations were designated for germplasm collection and conservation, special attention should be given to the minimum area required for seed collection. Considering the density of reproductive individuals in the FOR population (12 individuals ha^{-1}), for example, a minimum area for seed collection of c. 11.6 ha would be necessary. This would allow the collection of seeds in a way that maintains the long-term genetic diversity of the population without any considerations for minimum distances between seed trees given the lack coancestry observed among reproductive individuals. For GRA, the minimum necessary collection area, considering only the number of reproductive individuals in the population (17.7 individuals ha^{-1}), would be c. 7.5 ha. However, distances of less than 30 m between seed trees should be avoided given the significant coancestry observed among reproductive individuals in this population. Bearing in mind the strong aggregation of individuals observed in this population (i.e., non-random pattern in the spatial distribution of individuals), a substantially larger area for seed collection should be considered. In order to form populations with smaller effective population sizes such as $\widehat{N}_e$ of 50, 13 and 14 seed trees should be used for collection in GRA and FOR, respectively.

Considering the conservation status of *B. eriospatha* in both assessed habitat types, open grassland populations are likely under higher anthropogenic pressure due to cattle grazing and land conversion to silviculture, combined with a lack of legal protection, as these populations occur within productive agricultural sites. Forest *B. eriospatha* populations, on the other hand, are under a relatively lower threat due to the existence of forest protection laws (Atlantic Forest Law), but these populations are much rarer to find. In any case, conservation strategies should consider these two habitats. Besides proper seed collection and restoration actions, efforts for in situ and *ex situ* conservation must be prioritized, with a particular focus on promoting the natural establishment and survival of new seedlings in current populations. The general lack of regeneration in *B. eriospatha* populations, and therefore, lack of generation turnover, in addition to the mortality and poaching of senescent individuals (Candido-Ribeiro 2017; Nazareno and Reis 2014a), are likely the most important threats to the genetic conservation of the species. Finally, as exotic tree plantations, such as *Pinus* sp., expand across southern Brazilian landscapes, the effects of commercial forest plantations on the maintenance of genetic diversity within and among *B. eriospatha* populations should be investigated.

The main limitation of our study is the lack of replications within each habitat (i.e., forest and open grassland), which precludes the possibility of general inferences about the environments where these two populations occur.

Therefore, extrapolations of our results to other forest and open grassland *B. eriospatha* populations should be made with extreme caution. Furthermore, the diversity and genetic structure data related to the progeny should also be taken with some caution. Since we did not find sufficient seedlings to be sampled directly from the populations in their natural environments, seedlings were germinated under laboratory conditions, from seeds taken at random in each population, and therefore, seeds were not exposed to selection in their natural environmental conditions. However, the effort to estimate such parameters for this ontogenetic class was considered pertinent as it gave us some understanding about the genetic variation that is transmitted through generations in both *B. eriospatha* populations. Finally, we acknowledge that a larger set of polymorphic microsatellite markers would have enhanced the resolution of our analyses and provided more robust estimates of genetic diversity. Nevertheless, such markers are currently unavailable for the species.

Conclusions

The extinction risk facing *B. eriospatha* is driven by a synergistic combination of illegal poaching, habitat fragmentation, and the rapid expansion of exotic tree plantations. These pressures are exacerbated by cattle grazing, fruit consumption, and the senescence of adult individuals, leading to a critical lack of recruitment. Our findings suggest that adult mortality is the primary factor shaping the spatial distribution patterns of these populations. To mitigate this decline, it is essential to establish new populations while simultaneously protecting and enriching existing ones. Providing precise seed-collection guidelines—informed by our detailed characterization of genetic diversity and spatial genetic structure within forest and grassland habitats—will ensure that restoration efforts use populations with sufficient genetic diversity, increasing the adaptive potential in the species. Ultimately, conserving both habitat types is vital for the long-term persistence of *B. eriospatha*.

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Authors' contributions RCR and MSR conceived the study and the sampling design. RCR, TM, and NCFC collected the data, sampled the seeds, and collected tissue for DNA extractions. RCR performed the lab work and analyzed the data. RCR wrote the manuscript with inputs from TM, NCFC, and MSR. All authors have approved the final version of the manuscript.

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Data availability The dataset used in this study will be made available in Dryad upon the acceptance of the manuscript.

Declarations

Competing interests The authors declare no competing interests.

References

Aitken SN, Jordan R, Tumas HR (2024) Conserving evolutionary potential: combining landscape genomics with established methods to inform plant conservation. Annu Rev Plant Biol 75(1):707–736. https://doi.org/10.1146/annurev-arplant-070523-044239

Allendorf FW, Funk WC, Aitken SN, Byrne M, Luikart G, Antunes A (2022) Conservation and the Genomics of Populations. Oxford University Press, Oxford. https://doi.org/10.1093/oso/9780198856566.001.0001

Amorim E, Heiden G (2025) Butia eriospatha: The IUCN Red List of Threatened Species - e.T38462A236560664. In *IUCN Red List of Threatened Species*. https://doi.org/10.2305/IUCN.UK.2025-2.RLTS.T38462A236560664.pt

Andrade V, Casas A, Balslev H, Mora F (2024) The role of wild palms in agroforestry systems in the Neotropics: a review. People Nat 6(6):2200–2227. https://doi.org/10.1002/pan3.10741

Andreazzi CS, Pires AS, Fernandez FAS (2009) Mamíferos e palmeiras neotropicais: Interações em paisagens fragmentadas. Oecol Bras 13(4):554–574. https://doi.org/10.4257/oeco.2009.1304.02

Baddeley A, Rubak E, Turner R (2016) Spatial Point Patterns: Methodology and Applications with R, 1st edn. Chapman and Hall/CRC

Brancalion PHS, Niamir A, Broadbent E, Crouzeilles R, Barros FSM, Almeyda Zambrano AM, Baccini A, Aronson J, Goetz S, Leighton Reid J, Strassburg BBN, Wilson S, Chazdon RL (2019) Global restoration opportunities in tropical rainforest landscapes. Sci Adv 5(7):1–11. https://doi.org/10.1126/sciadv.aav3223

Browne L, Ottewell K, Karubian J (2015) Short-term genetic consequences of habitat loss and fragmentation for the neotropical palm *Oenocarpus bataua*. Heredity 115(5):389–395. https://doi.org/10.1038/hdy.2015.35

Calambás-Trochez LF, Velazco SJE, Hoffmann PM, Gurski EM, Brum FT, Carlucci MB (2021) Climate and land-use changes coupled with low coverage of protected areas threaten palm species in South Brazilian grasslands. Perspect Ecol Conserv 19(3):345–353. https://doi.org/10.1016/j.pecon.2021.03.010

Candido-Ribeiro R (2017) Aspectos históricos, demográficos, morfológicos e genéticos de populações de Butia eriospatha (Martius ex. Drude) Beccari (Arecaceae) em paisagens contrastantes no planalto serrano de Santa Catarina. Universidade Federal de Santa Catarina

Candido-Ribeiro R, Lauterjung MB, Montagna T, Bernardi AP, da Costa NCF, Hoeltgebaum MP, dos Reis MS (2019) Distinct seeds in contrasting habitats: morphological and reproductive responses in *Butia eriospatha* to new environmental conditions. Acta Oecol 99:103447. https://doi.org/10.1016/j.actao.2019.103447

Choo J, Juenger TE, Simpson BB (2012) Consequences of frugivore-mediated seed dispersal for the spatial and genetic structures of a neotropical palm. Mol Ecol 21(4):1019–1031. https://doi.org/10.1111/j.1365-294X.2011.05425.x

Cockerham CC (1969) VARIANCE OF GENE FREQUENCIES. Evolution 23(1):72–84. https://doi.org/10.1111/j.1558-5646.1969.tb03496.x

Conceição TA, Santos AS, Fernandes AKC, Meireles GN, de Oliveira FA, Barbosa RM, Gaiotto FA (2024) Guiding seed movement: environmental heterogeneity drives genetic differentiation in *Plathymenia reticulata*, providing insights for restoration. AoB Plants. https://doi.org/10.1093/aobpla/plae032

CONSEMA-SC (2014) *CONSEMA-SC. Conselho Estadual do Meio Ambiente de Santa Catarina. Resolução no 51, 5 de dezembro de 2014.*

Costa NCF, Stedille LIB, Lauterjung MB, Mantovani A, Nodari RO (2019) Distinguishing mutations and null alleles from genotyping errors using mother progeny comparisons in Brazilian pine (*Araucaria angustifolia*). Tree Genet Genomes. https://doi.org/10.1007/s11295-019-1388-8

Costa N, Stedille LIB, Busarello M, Montagna T, Candido-Ribeiro R, Paulo A, Mantovani A, Sedrez M, Nodari RO (2021) Spatiotemporal variation in mating system and genetic diversity of *Araucaria angustifolia*: implications for conservation and seed collection. For Ecol Manage. https://doi.org/10.1016/j.foreco.2020.118716

Cottrell JE, Vaughan SP, Connolly T, Sing L, Moodley DJ, Russell K (2009) Contemporary pollen flow, characterization of the maternal ecological neighbourhood and mating patterns in wild cherry (*Prunus avium* L.). Heredity 103(2):118–128. https://doi.org/10.1038/hdy.2009.39

Da Silva Carvalho C, Ribeiro MC, Côrtes MC, Galetti M, Collevatti RG (2015) Contemporary and historic factors influence differently genetic differentiation and diversity in a tropical palm. Heredity 115(3):216–224. https://doi.org/10.1038/hdy.2015.30

Degen B, Sebbenn AM (2016) Genetics and Tropical Forests. In *Tropical Forestry Handbook* (pp. 885–920). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-54601-3_75

de Lima RAF, Dauby G, de Gasper AL, Fernandez EP, Vibrans AC, de Oliveira AA, Prado PI, Souza VC, de Siqueira MF, ter Steege H (2024) Comprehensive conservation assessments reveal high extinction risks across Atlantic Forest trees. Science 383(6679):219–225. https://doi.org/10.1126/science.abq5099

de Lima RAF, Oliveira AA, Pitta GR, de Gasper AL, Vibrans AC, Chave J, ter Steege H, Prado PI (2020) The erosion of biodiversity and biomass in the Atlantic Forest biodiversity hotspot. Nat Commun 11(1):1–16. https://doi.org/10.1038/s41467-020-20217-w

Doyle JJ, Doyle JL (1990) A rapid total DNA preparation procedure for fresh plant tissue. Focus 12(1):13–15

Exposito-Alonso M, Booker TR, Czech L, Gillespie L, Hateley S, Kyriazis CC, Lang PLM, Leventhal L, Nogues-Bravo D, Pagowski V, Ruffley M, Spence JP, Toro Arana SE, WeiÃŸ CL, Zess E (2022) Genetic diversity loss in the Anthropocene. Science 377(6613):1431–1435. https://doi.org/10.1126/science.abn5642

Frichot E, François O (2015) LEA: an R package for landscape and ecological association studies. Methods Ecol Evol 6(8):925–929. https://doi.org/10.1111/2041-210X.12382

Galetti M, Zipparro VB, Morellato PC (1999) Fruiting phenology and frugivory on the palm *Euterpe edulis* in a lowland Atlantic Forest of Brazil. Ecotropica 5:115–122

Goudet J (1995) FSTAT (version 2.9.3.2–2002): a computer program to calculate F-statistics. J Hered 86(6):485–486

Guo SW, Thompson EA (1992) Performing the exact test of Hardy-Weinberg proportion for multiple alleles. Biometrics 48(2):361–372

Hardy OJ, Vekemans X (2002) SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. Mol Ecol Notes 2(4):618–620. https://doi.org/10.1046/j.1471-8286.2002.00305.x

Hartl DL, Clark AG (1997) Principles of population genetics. Fourth). Sinauer associates

Hoban S, Campbell CD, da Silva JM, Ekblom R, Funk WC, Garner BA, Godoy JA, Kershaw F, MacDonald AJ, Mergeay J, Minter M, O'Brien D, Vinas IP, Pearson SK, Pérez-Espona S, Potter KM, Russo IRM, Segelbacher G, Vernesi C, Hunter ME (2021) Genetic diversity is considered important but interpreted narrowly in country reports to the Convention on Biological Diversity: current actions and indicators are insufficient. Biol Conserv. https://doi.org/10.1016/j.biocon.2021.109233

Hoban S, da Silva JM, Mastretta-Yanes A, Grueber CE, Heuertz M, Hunter ME, Mergeay J, Paz-Vinas I, Fukaya K, Ishihama F, Jordan R, Köppä V, Latorre-Cárdenas MC, MacDonald AJ, Rincon-Parra V, Sjögren-Gulve P, Tani N, Thurfjell H, Laikre L (2023) Monitoring status and trends in genetic diversity for the Convention on Biological Diversity: an ongoing assessment of genetic indicators in nine countries. Conserv Lett 16(3):1–12. https://doi.org/10.1111/conl.12953

Hutchings MJ (1997) The Structure of Plant Populations. In M. J. Crawley (Ed.), *Plant Ecology* (Second, pp. 325–358). Wiley. https://doi.org/10.1002/9781444313642

Johnson DV (1988) Worldwide Endangerment of Useful Palms. In M. J. Balick (Ed.), *The Palm – Tree of Life: Biology, Utilization and Conservation (Advances in Economic Botany, Vol. 6)* (p. 282)

Joly CA, Metzger JP, Tabarelli M (2014) Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. New Phytol 204(3):459–473. https://doi.org/10.1111/nph.12989

Jordan R, Breed MF, Prober SM, Miller AD, Hoffmann AA (2019) How well do revegetation plantings capture genetic diversity? Biol Lett. https://doi.org/10.1098/rsbl.2019.0460

Jordan R, Harrison PA, Breed M (2024) The eco-evolutionary risks of not changing seed provenancing practices in changing environments. Ecol Lett 27(1):1–6. https://doi.org/10.1111/ele.14348

Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error

increases success in paternity assignment. Mol Ecol 16(5):1099–1106. https://doi.org/10.1111/j.1365-294X.2007.03089.x

Kardos M, Armstrong EE, Fitzpatrick SW, Hauser S, Hedrick PW, Miller JM, Tallmon DA, Chris Funk W (2021) The crucial role of genome-wide genetic variation in conservation. Proc Natl Acad Sci U S A. https://doi.org/10.1073/pnas.2104642118

Lanes ÉCM, Motoike SY, Kuki KN, Resende MDV, Caixeta ET (2016) Mating system and genetic composition of the macaw palm (acrocomia aculeata): implications for breeding and genetic conservation programs. J Hered 107(6):527–536. https://doi.org/10.1093/jhered/esw038

Lewis PO, Zaykin D (2002) *GDA-Genetic Data Analysis: version 1.1*

Li CC (1976) First course in population genetics. Boxwood

Loiselle BA, Sork VL, Nason J, Graham C (1995) Spatial genetic structure of a tropical understory shrub, *Psychotria officinalis* (Rubiaceae). Am J Bot 82(11):1420. https://doi.org/10.2307/2445869

Macía MJ, Armesilla PJ, Cámara-Leret R, Paniagua-Zambrana N, Villalba S, Balslev H, Pardo-de-Santayana M (2011) Palm uses in northwestern South America: a quantitative review. Bot Rev 77(4):462–570. https://doi.org/10.1007/s12229-011-9086-8

MapBiomas (2025) MapBiomas Project—Collection 10 of the Annual Land Use Land Cover Maps of Brazil. https://brasil.mapbiomas.org/

Marchioro CA, da Silva Krechemer F, dos Santos KL, Siminski A (2023) Biotic interactions under risk: climate change drives spatial mismatch between a critically endangered tree and its seed dispersers and predators. Clim Change 176(12):1–20. https://doi.org/10.1007/s10584-023-03642-w

Montagna T, Lauterjung MB, Candido-Ribeiro R, da Silva JZ, Hoeltgebaum MP, da Costa NCF, Bernardi AP, dos Reis MS (2018) Spatial genetic structure, population dynamics, and spatial patterns in the distribution of *Ocotea catharinensis* from southern Brazil: implications for conservation. Can J For Res 48(5):506–516. https://doi.org/10.1139/cjfr-2017-0446

Montagna T, Lauterjung MB, Costa N, Bernardi AP, Candido-Ribeiro R, Reis M (2019) Guidelines for seed collection of *Araucaria angustifolia* (Bertol.) Kuntze: a genetic, demographic and geographic approach. For Ecol Manage 438:10–17. https://doi.org/10.1016/j.foreco.2019.02.006

Mourelle D, Gaiero P, Speroni G, Millán C, Gutiérrez L, Mazzella C (2016) Comparative pollen morphology and viability among endangered species of *Butia* (Arecaceae) and its implications for species delimitation and conservation. Palynology 40(2):160–171. https://doi.org/10.1080/01916122.2014.999955

Muscarella R, Emilio T, Phillips OL, Lewis SL, Slik F, Baker WJ, Couvreur TLP, Eiserhardt WL, Svenning J, Affum-Baffoe K, Aiba S, de Almeida EC, de Almeida SS, de Oliveira EA, Álvarez-Dávila E, Alves LF, Alvez-Valles CM, Carvalho FA, Guarin FA, Svenning J-C, Aiba S-I, Andrade A, Aragão LEOC, Murakami AA, Arroyo L, Ashton PS, Corredor GAA, Baker TR, de Camargo PB, Barlow J, Bastin J-F, Bengone NN, Berenguer E, Berry N, Blanc L, Böhning-Gaese K, Bonal D, Bongers F, Bradford M, Brambach F, Brearley FQ, Brewer SW, Camargo JLC, Campbell DG, Castilho CV, Castro W, Catchpole D, Cerón Martínez CE, Chen S, Chhang P, Cho P, Chutipong W, Clark C, Collins M, Comiskey JA, Medina MNC, Costa FRC, Culmsee H, David-Higuita H, Davidar P, del Aguila-Pasquel J, Derroire G, Di Fiore A, Van Do T, Doucet J-L, Dourdain A, Drake DR, Ensslin A, Erwin T, Ewango CEN, Ewers RM, Fauset S, Feldpausch TR, Ferreira J, Ferreira LV, Fischer M, Franklin J, Fredriksson GM, Gillespie TW, Gilpin M, Gonmadje C, Gunatilleke AUN, Hakeem KR, Hall JS, Hamer KC, Harris DJ, Harrison RD, Hector A, Hemp A, Herault B, Pizango CGH, Coronado ENH, Hubau W, Hussain MS, Ibrahim F-H, Imai N, Joly CA, Joseph S, K A, Kartawinata K, Kassi J, Killeen TJ, Kitayama K, Klitgård BB, Kooyman R, Labrière N, Larney E, Laumonier Y, Laurance SG, Laurance WF, Lawes MJ, Levesley A, Lisingo J, Lovejoy T, Lovett JC, Lu X, Lykke AM, Magnusson WE, Mahayani NPD, Malhi Y, Mansor A, Peña JLM, Marimon-Junior BH, Marshall AR, Melgaco K, Bautista CM, Mihindou V, Millet J, Milliken W, Mohandass D, Mendoza ALM, Mugerwa B, Nagamasu H, Nagy L, Seuaturien N, Nascimento MT, Neill DA, Neto LM, Nilus R, Vargas MPN, Nurtjahya E, de Araújo RNO, Onrizal O, Palacios WA, Palacios-Ramos S, Parren M, Paudel E, Morandi PS, Pennington RT, Pickavance G, Pipoly JJ, Pitman NCA, Poedjirahajoe E, Poorter L, Poulsen JR, Rama Chandra Prasad P, Prieto A, Puyravaud J-P, Qie L, Quesada CA, Ramírez-Angulo H, Razafimahaimodison JC, Reitsma JM, Requena-Rojas EJ, Correa ZR, Rodriguez CR, Roopsind A, Rovero F, Rozak A, Lleras AR, Rutishauser E, Rutten G, Punchi-Manage R, Salomão RP, Van Sam H, Sarker SK, Satdichanh M, Schietti J, Schmitt CB, Marimon BS, Senbeta F, Nath Sharma L, Sheil D, Sierra R, Silva-Espejo JE, Silveira M, Sonké B, Steininger MK, Steinmetz R, Stévart T, Sukumar R, Sultana A, Sunderland TCH, Suresh HS, Tang J, Tanner E, ter Steege H, Terborgh JW, Theilade I, Timberlake J, Torres-Lezama A, Umunay P, Uriarte M, Gamarra LV, van de Bult M, van der Hout P, Martinez RV, Vieira ICG, Vieira SA, Vilanova E, Cayo JV, Wang O, Webb CO, Webb EL, White L, Whitfeld TJS, Wich S, Willcock S, Wiser SK, Young KR, Zakaria R, Zang R, Zartman CE, Zo-Bi IC, Balslev H (2020) The global abundance of tree palms. Glob Ecol Biogeogr 29(9):1495–1514. https://doi.org/10.1111/geb.13123

Nazareno AG, dos Reis MS (2014a) Where did they come from? Genetic diversity and forensic investigation of the threatened palm species *Butia eriospatha*. Conserv Genet 15(2):441–452. https://doi.org/10.1007/s10592-013-0552-1

Nazareno AG, Dos Reis MS (2014b) At risk of population decline? An ecological and genetic approach to the threatened palm species *Butia eriospatha* (Arecaceae) of southern Brazil. J Hered 105(1):120–129. https://doi.org/10.1093/jhered/est065

Nazareno AG, Reis MS (2012) Linking phenology to mating system: exploring the reproductive biology of the threatened palm species *Butia eriospatha*. J Hered 103(6):842–852. https://doi.org/10.1093/jhered/ess070

Nazareno AG, Zucchi MI, dos Reis MS (2011) Microsatellite markers for *Butia eriospatha* (Arecaceae), a vulnerable palm species from the Atlantic Rainforest of Brazil. Am J Bot 98(7):198–200. https://doi.org/10.3732/ajb.1100064

Newbold T, Hudson LN, Hill SLL, Contu S, Lysenko I, Senior RA, Börger L, Bennett DJ, Choimes A, Collen B, Day J, De Palma A, Díaz S, Echeverria-Londoño S, Edgar MJ, Feldman A, Garon M, Harrison MLK, Alhusseini T, Ingram DJ, Itescu Y, Kattge J, Kemp V, Kirkpatrick L, Kleyer M, Correia DLP, Martin CD, Meiri S, Novosolov M, Pan Y, Phillips HRP, Purves DW, Robinson A, Simpson J, Tuck SL, Weiher E, White HJ, Ewers RM, Mace GM, Scharlemann J, Purvis A (2015) Global effects of land use on local terrestrial biodiversity. Nature 520(7545):45–50. https://doi.org/10.1038/nature14324

Ottewell K, Grey E, Castillo F, Karubian J (2012) The pollen dispersal kernel and mating system of an insect-pollinated tropical palm, *Oenocarpus bataua*. Heredity 109(6):332–339. https://doi.org/10.1038/hdy.2012.40

Paquette SR (2012) *PopGenKit: Useful functions for (batch) file conversion and data resampling in microsatellite datasets* (R package version 1)

Peakall R, Smouse PE (2012) GenALEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research-an update. Bioinformatics 28(19):2537–2539. https://doi.org/10.1093/bioinformatics/bts460

Perdomo O, Becker R, Singer RB (2024) Pollination ecology, breeding system, and conservation of *Butia lallemantii* Deble & Marchiori

(Arecaceae): a useful dwarf palm tree from the Pampa. Plants. https://doi.org/10.3390/plants13111562
R Core Team (2021) A language and environment for statistical computing. R Foundation for Statistical Computing
Ramos SLF, Lopes MTG, Lopes R, Cunha R, Macêdo J, Contim LAS, Clement CR, Rodrigues DP, Bernardes LG (2011) Determination of the mating system of Tucumã palm using microsatellite markers. Crop Breed Appl Biotechnol 11(2):181–185. https://doi.org/10.1590/s1984-70332011000200011
Reis A, Zambonin RM, Nakazono EM (1999) Recuperação de áreas florestais degradadas utilizando a sucessão e as interações planta-animal. Série Cadernos Da Reserva Da Biosfera Da Mata Atlântica 14:1–41
Reis M, Mantovani A, Silva J, Mariot A, Bittencourt R, Nazareno AG, Ferreira DK, Steiner F, Montagna T, Silva F, Fernandes CD, Altrak G, Figueredo LGU (2012) Distribuição da Diversidade Genética e Conservação de EspéciesArbóreas em Remanescentes Florestais de Santa Catarina. In: Vibrans AC, Sevegnani L, de Gasper AL, Lingner DV (eds) Inventário florístico florestal de Santa Catarina, volume 1: Diversidade e conservação dos remanescentes florestais. Edifurb, Blumenau, pp 143–169
Reitz R (1974) Palmeiras. (Flora Ilustrada Catarinense-PALM). Herbário Barbosa Rodrigues
Ripley BD (1977) Modelling spatial patterns. J Royal Stat Soc Ser B: Stat Methodol 39(2):172–192. https://doi.org/10.1111/j.2517-6161.1977.tb01615.x
Ritland K (1989) Correlated matings in the partial selfer *Mimulus guttatus*. Evolution 43(4):848–859. https://doi.org/10.1111/j.1558-5646.1989.tb05182.x
Ritland K (2009) Mating system program - MLTR (version 3.4). https://doi.org/10.13140/RG.2.2.14456.57608
Ritland K, Jain S (1981) A model for the estimation of outcrossing rate and gene frequencies using n independent loci. Heredity 47(1):35–52. https://doi.org/10.1038/hdy.1981.57
Rodríguez-Peña RA, Jestrow B, Cinea W, Veloz A, Jiménez-Rodríguez F, García R, Meerow AW, Griffith MP, Maunder M, Francisco-Ortega J (2014) Conservation and genetics of two Critically Endangered Hispaniolan palms: genetic erosion of *Pseudophoenix lediniana* in contrast to *P. ekmanii*. Plant Syst Evol 300(9):2019–2027. https://doi.org/10.1007/s00606-014-1028-6
Rodrigues I, Scussel GF, Bernardi A, Thalmayr P, Ferreira JM, Silva A, Mantovani A, Reis MSD, Montagna T (2023) Autoecology, diversity, and internal genetic structure of *Ocotea porosa* (nees & mart.) Barroso: subsidies for seed collection. Rev Arvore 47:1–12. https://doi.org/10.1590/1806-908820230000030
Romulo CL, Gilmore MP, Endress BA, Horn C (2022) *Mauritia flexuosa* fruit production increases with increasing palm height in the Peruvian Amazon. Plants People Planet 4(6):599–604. https://doi.org/10.1002/ppp3.10299
Rousset F (2008) GENEPOP'007: a complete re-implementation of the GENEPOP software for Windows and Linux. Mol Ecol Resour 8(1):103–106. https://doi.org/10.1111/j.1471-8286.2007.01931.x
Santos AS, Cazetta E, Morante Filho JC, Baumgarten J, Faria D, Gaiotto FA (2015) Lessons from a palm: genetic diversity and structure in anthropogenic landscapes from Atlantic Forest, Brazil. Conserv Genet 16(6):1295–1302. https://doi.org/10.1007/s10592-015-0740-2
Sebbenn AM (2002) Número De Árvores Matrizes E Conceitos Genéticos Na Coleta De Sementes Para Reflorestamentos Com Espécies Nativas. Rev Inst Florestal 14(2):115–132. https://doi.org/10.24278/2178-5031.2002142412
Sebbenn AM (2006) Sistema de reprodução em espécies arbóreas tropicais e suas implicações para a seleção de árvores matrizes para reflorestamentos ambientais. In: Higa AR, Silva LD (eds) Pomares de sementes de espécies nativas. FUPEF
Seibold S, Gossner MM, Simons NK, Blüthgen N, Müller J, Ambarlı D, Ammer C, Bauhus J, Fischer M, Habel JC, Linsenmair KE, Nauss T, Penone C, Prati D, Schall P, Schulze ED, Vogt J, Wöllauer S, Weisser WW (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574(7780):671–674. https://doi.org/10.1038/s41586-019-1684-3
SEMA-RS (2014) *SEMA-RS. Secretaria do Meio Ambiente do Rio Grande do Sul. Decreto no 52.109, 01/12/2014, 2014.*
Seoane CES, Kageyama PY, Ribeiro A, Matias R, Reis M, Bawa K, Sebbenn AM (2005) EFEITOS DA FRAGMENTAÇÃO FLORESTAL SOBRE A IMIGRAÇÃO DE SEMENTES E A ESTRUTURA GENÉTICA TEMPORAL DE POPULAÇÕES DE *Euterpe edulis* Mart. Rev Inst Florestal 17(1):25–43. https://doi.org/10.24278/2178-5031.2005171470
Silva KE, Martins SV, Santos NT, Ribeiro CAAS (2012) Padrões espaciais de espécies arbóreas tropicais. In: Martins SV (ed) Ecologia de florestas tropicais do Brasil. UFV, pp 216–244
Sosinski ÊE, Urruth LM, Barbieri RL, Marchi MM, Martens SG (2019) On the ecological recognition of *Butia* palm groves as integral ecosystems: why do we need to widen the legal protection and the in situ/on-farm conservation approaches? Land Use Policy 81:124–130. https://doi.org/10.1016/j.landusepol.2018.10.041
Sousa VA, Sebbenn AM, Hattemer HH, Ziehe M (2005) Correlated mating in populations of a dioecious Brazilian conifer, *Araucaria angustifolia* (Bert.) O. Ktze. For Genet 12(2):107–119
Thomas E, Jalonen R, Loo J, Boshier D, Gallo L, Cavers S, Bordács S, Smith P, Bozzano M (2014) Genetic considerations in ecosystem restoration using native tree species. For Ecol Manage 333(2014):66–75. https://doi.org/10.1016/j.foreco.2014.07.015
Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 4(3):535–538. https://doi.org/10.1111/j.1471-8286.2004.00684.x
Vekemans X, Hardy OJ (2004) New insights from fine-scale spatial genetic structure analyses in plant populations. Mol Ecol 13(4):921–935. https://doi.org/10.1046/j.1365-294X.2004.02076.x
Wagner JG, dos Santos KL, Heiden G, Vizzotto M, Barbieri RL (2025) Exploring the sociocultural importance of *Butia eriospatha* (Arecaceae), an iconic palm of the highlands of southern Brazil. Econ Bot. https://doi.org/10.1007/s12231-025-09642-4
Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38(6):1358–1370
Willson MF (1993) Dispersal mode, seed shadows, and colonization patterns. Vegetatio 107(1):261–280. https://doi.org/10.1007/BF00052229
Zechini AA, Lauterjung MB, Candido-Ribeiro R, Montagna T, Bernardi AP, Hoeltgebaum MP, Mantovani A, dos Reis MS (2018) Genetic conservation of Brazilian pine (*Araucaria angustifolia*) through traditional land use. Econ Bot 72(2):166–179. https://doi.org/10.1007/s12231-018-9414-6