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Structure and genetic diversity of *Anacardium humile* (Anacardiaceae): a tropical shrub

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ABSTRACT. *Anacardium humile* Saint Hilaire is a tropical shrub native to the Cerrado biome. It is a fruiting species with biological, medicinal, and socioeconomic significance. Thus, knowing how the genetic variability of natural populations is organized allows for the establishment of strategies for conservation and the sustainable use of the species and its biome. Six microsatellite loci previously developed from *Anacardium occidentale* were used to investigate the spatial genetic structure and genetic diversity of eight natural *A. humile* populations based on analyses of 242 adult plants. The results obtained indicate that these populations show a high level of genetic diversity (expected heterozygosity = 0.710). The endogamy coefficient was positive and significant for most populations, with a mean of 0.142 (P = 0.001). The genetic differentiation between populations was low (θ = 0.075 and G_{ST} = 0.066) but significant (P = 0.0001). The genotypes

of five of the eight populations were non-randomly distributed with clusters of related plants for which the coancestry values were positive and significant. These populations exhibited high and significant endogamy indices. The results obtained for *A. humile* populations show that genetic conservation programs should be implemented to maintain this species.

Key words: Cashew of Cerrado; Microsatellite markers; Cerrado; Structure and genetic diversity

INTRODUCTION

Changes in tropical landscapes resulting from fragmentation accentuate the loss of genetic diversity as they reduce population sizes. When small populations become isolated and thus more susceptible to effects associated with endogamy, genetic drift, and absent and/or limited gene flow (Frankham et al., 2002), and also the capacity of a species to evolve suffers (Hamrick, 2004). Therefore, maintaining genetic diversity is critical, as it is a fundamental component of biological diversity and allows species to adapt to environments through a constant process of transformation (Frankham et al., 2002).

In recent years, tropical biomes have been greatly degraded, making their conservation of utmost importance. This is especially true for the Cerrado, the second largest Brazilian biome, which contains great biological diversity and many habitats and is the source of various natural resources (Cavalcanti and Joly, 2002). The Cerrado is considered a global biodiversity hotspot based on the anthropic impacts it has suffered, the number of endemic species it houses, and the high level of species diversity in general (Myers et al., 2000).

The Cerrado has suffered great damage from alterations to its landscape due to the expansion of human activities in the region, such as the use of the land for agriculture and ranching, exploitation of the native flora and fauna, and predatory extractivism (Henriques, 2003). These activities have put the biodiversity of Cerrado at risk, and early studies on this topic looked at the accelerated fragmentation of its natural habitats (Machado et al., 2004). Thus, the Cerrado is an interesting region for studying the effects of human occupation on the genetics of plant populations and how genetic variation relates to the characteristics of life history (Collevatti et al., 2010).

Numerous studies on the genetic conservation of native Cerrado plant species have been carried out, analyzing these populations using microsatellite molecular markers (Zucchi et al., 2003; Moura et al., 2009; Collevatti et al., 2010; Tarazi et al., 2010). This technique is widely used because it is codominant, highly polymorphic and informative (Tautz, 1989; Guichoux et al., 2011).

Interest in genetic studies of natural populations that combine evolutionary biology and ecology has increased in recent years (Frankham et al., 2002). Quantifying the levels of genetic diversity and understanding how populations are genetically structured allow for the identification of populations and priority sites for conservation. Additionally, it is possible to monitor long-term changes in gene flow, endogamy levels, genetic structure, and effective population sizes of species in altered habitats and/or exploited species (Gibbs, 2001; Frankham et al., 2002). These conservation activities integrate genetics with demographic and environmental variables, catastrophes, and human impact to predict extinction risks, and compare alternative options in species recovery programs (Frankham, 2003).

This study aims to assess how natural populations of *Anacardium humile*, an important tropical shrub species native to the Cerrado biome, are genetically structured. The level of genetic diversity was quantified in these populations to obtain information for the conservation, management, and appropriate use of the species and its biome.

MATERIAL AND METHODS

Species studied

A. humile Saint Hilaire is a tropical fruiting species in the Anacardiaceae family. The species is commonly known as cashew of Cerrado because it is native to rocky savannas in the Cerrado biome (Almeida et al., 1998). The *A. humile* is a hermaphroditic shrub measuring up to 80 cm (Almeida et al., 1998), with white flowers, diurnal anthesis, a nectar scent, and is pollinated by small insects such as bees and butterflies (Martins and Batalha, 2006). However, there are no detailed studies on its reproductive system. The cashew of *A. humile* has similar features and use of the related species cashed nut *Anacardium occidentale*, the only species of cashew tree cultivated in tropics. As with the *A. humile*, other species of the genus are native and exploited by extractivism. The pseudo fruit of *A. humile* has an acidic flavor and juicy white pulp and is consumed *in natura* or in the form of juices, sweets, and jams. Nearly all parts of the plant are used in folk medicine (Almeida et al., 1998; Vieira et al., 2006; Porto et al., 2008).

A. humile is a heliophile with a subterraneous stem that can stretch nearly 20 m. The stem stores water, allows the species to withstand long droughts and protects it from fires. Thus, the species has features that make it resistant to the particular environmental water stresses of the Cerrado (Almeida et al., 1998).

Study areas

Eight natural *A. humile* populations were selected from the Cerrado biome in the North of Minas Gerais State (Figure 1). Two populations (BAL and CAT) were in a conservation unit (APA Pandeiros) (IEF - Instituto Estadual de Florestas, 2011). The other six populations were from diversified areas and private properties that predominantly had Cerrado vegetation, with some areas that had pastures and had undergone native flora lumber extraction, while others were in a better state of conservation (Table 1). The physiognomic features of Cerrado biome were classified according to Bitencourt et al. (1997). The method proposed by Santos and Vieira (2005) was used to assess the conservation state of the sampling areas, which involved assessing the presence of livestock, fire, and selective cutting to assign a score from 1 to 5 for each area (Table 1).

Sampling, DNA extraction, and microsatellite analysis

A total of 242 *A. humile* adult plants were collected from the eight populations and georeferenced (Table 1). The minimum distance between plants collected within a population set was approximately 50 m, given that the stem is subterraneous and could stretch up to 20 m in diameter. Young leaves were collected from each plant for DNA extraction following the protocol proposed by Doyle and Doyle (1987).

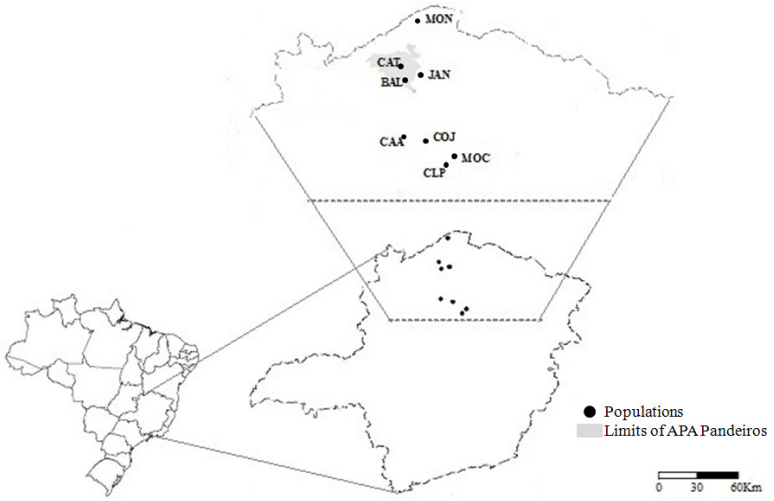

Figure 1. Geographic distribution of the *Anacardium humile* populations in North of Minas Gerais State. For population names, see Table 1.

Table 1. Geographical location and sampling details of the *Anacardium humile* populations studied.

Populations	Population code	Coordinates	Sample size	Cerrado physiognomies	PS
Montalvânia	MON	14°29''899"S 44°33'106"W	31	Open cerrado	3
Coração de Jesus	COJ	16°34'128"S 44°24'466"W	30	Cerrado *sensu stricto*	5
Montes Claros	MOC	16°50'615"S 43°55'531"W	30	Open cerrado	2
Januária	JAN	15°26'493"S 44°28'434"W	30	Closed cerrado	3
APA Pandeiros	BAL	15°30'871"S 44°45'176"W	30	Closed cerrado	5
APA Pandeiros	CAT	15°17'336"S 44°49'457"W	31	Closed cerrado	5
Claro dos Poções	CLP	16°59'395"S 44°04'198"W	30	Open cerrado	2
Campo Azul	CAA	16°30'271"S 44°46'113"W	30	Closed cerrado	3
Total			242		

PS = preservation status of the area (method proposed by Santos and Vieira, 2005).

Six microsatellite loci previously developed for *A. occidentale* (Croxford et al., 2006) and transferred to *A. humile* (Cota et al., 2012) were used in population genetic analyses (Table 2). The 15-µL reactions, containing 1X buffer (10 mM Tris-HCl, pH 8.4, 50 mM KCl), 0.7 µM of each primer, 250 µM of each dNTP, 1 U Taq DNA polymerase, 0.25 mg BSA, 1.0 to 1.6 mM $MgCl_2$, 1.25 to 3% formamide, and 9 ng DNA were PCR-amplified using a Veriti thermocycler (Applied Biosystems). The PCR protocol consisted of an initial denaturation at 94°C for 5 min, followed by 35 cycles of denaturation at 94°C for 1 min, annealing at the primer-specific temperature for 1 min, and extension at 72°C for 1 min, and a final extension at 72°C for 7 min.

The amplified products were separated on 5% denaturing polyacrylamide gels stained with 1 mg/mL ethyl bromide. The size of the alleles was determined by comparison to a standard 50-bp molecular weight marker.

Data analysis

The genetic diversity was estimated from the number of alleles per locus (N_A), the

observed heterozygosity (H_O), the expected heterozygosity (H_E) under the Hardy-Weinberg equilibrium, and the endogamy coefficient (f), which were estimated using the Genetic Data Analysis - GDA 1.1 software (Lewis and Zaykin, 2001). The deviation from the Hardy-Weinberg equilibrium and test for linkage disequilibrium for pairs of loci were assessed using the FSTAT 2.9.3.2 software using permutations with the Bonferroni correction (Goudet, 2002).

Table 2. Characterization of six microsatellite loci in *Anacardium humile.*

Locus	Sequence (5'-3')	Repeat motif	AT (°C)
mAoR6	F: CAAAACTAGCCGGAATCTAGC	$(AT)_5(GT)_{12}$	58.2
	R: CCCCATCAAACCCTTATGAC		
mAoR17	F: GCAATGTGCAGACATGGTTC	$(GA)_{24}$	56.1
	R: GGTTTCGCATGGAAGAAGAG		
mAoR29	F: GGAGAAGAAAAGTTAGGTTTGAC	$(TG)_{10}$	61
	R: CGTCTTCTTCCACATGCTTC		
mAoR46	F: CGGCGTCGTTAAAGCAGT	$(ACC)_7(AC)_3$	61
	R: TCCTCCTCCGTCTCACTTTC		
mAoR52	F: GCTATGACCCTTGGGAACTC	$(GT)_{16}(TA)_2$	60
	R: GTGACACAACCAAAACCACA		
mAoR55	F: TGACTTTCAAATGCCACAAC	$(AT)_8CT(AC)_5$	60
	R: CTCAAGCTTTCATGGGGATT		

AT = annealing temperature.

To test whether populations were differentiated, the genetic structure was estimated from the coancestry coefficients of Weir and Cockerham (1984). The coefficients were estimated from the variance of allelic frequencies for the individual plants, with F (total endogamy coefficient), f (endogamy coefficient), and θ (differentiation between populations), using the FSTAT 2.9.3.2 software, based on 1000 randomizations with the Bonferroni correction (Goudet, 2002).

The genetic differentiation between populations was also estimated using the G_{ST} index, which is a better measure of genetic differentiation for the mutation rates of microsatellite loci, using the FSTAT 2.9.3.2 software (Goudet, 2002). The significance of the differentiation test was estimated by randomization of the genotypes among the samples to obtain the G log-likelihood statistic (Goudet, 2002). The genetic differentiation (θ) between populations was used as the basis for constructing a dendrogram using the UPGMA (unweighted pair-group method with arithmetic averages) method using the NTSYS program, version 2.11X (Rohlf, 2000).

To graphically visualize the differences between the populations, the genetic distance matrix, calculated according to Nei (1978), was used to construct a principal component analysis (PCA) using the GenAlEx 6.1 software (Peakall and Smouse, 2006). The hypothesis of genetic isolation by geographic distance was assessed by the Mantel test using the GenAlEx 6.1 software (Peakall and Smouse, 2006), taking into account the relationship between the Nei genetic distance and the geographic distance (km) among *A. humile* population pairs.

The spatial genetic structure (SGS) of genotypes within populations was analyzed based on the estimated coancestry coefficient. The coancestry value was estimated from the coefficient of kinship between pairs of plants within each population for 10 distinct distance classes, which were not defined *a priori*, using the SPAGeDI program, version 1.2 (Hardy and Vekemans, 2002).

Confidence intervals were constructed at 95% probability of the standard error of the mean for the estimates obtained by jackknife resampling, from the estimated mean coancestry coefficient for the distance classes, according to Hardy and Vekemans (2002). One thousand permutations were performed within each class to test for the occurrence of SGS, and its

magnitude was calculated using the following formula (Vekemans and Hardy, 2004): $Sp = -b_{log} / (1 - F_{ij(1)})$, where b_{log} is the slope of the regression curve for the coancestry coefficient and $F_{ij(1)}$ is the value of the coancestry coefficient for the first distance class (F_{ij}) for all loci. The values for *Sp* were used to compare the extent of spatial genetic structuring between populations.

RESULTS

Diversity and genetic structure

The six microsatellite loci evaluated for the *A.humile* populations produced an average of 5.2 alleles per population (Table 3). The H_O was lower than the H_E for most populations, except for the COJ population. The mean H_O and H_E were 0.611 and 0.710, respectively (Table 3). The relationship between the H_O and H_E resulted in high and significant endogamy coefficients (*f*) for the JAN, BAL, CAT, CLP, and CAA populations. Non-significant values for *f* were found for the MON, MOC, and COJ populations. The COJ population had a negative *f* value, suggesting the absence of endogamy and a high proportion of heterozygotes, as estimated by H_O. Nevertheless, the mean of *f* was positive and significant for the *A. humile* populations (Table 3). No pair of loci exhibited linkage disequilibrium in the populations analyzed (P = 0.000042) based on 1000 permutations with the Bonferroni correction.

Table 3. Genetic diversity of the eight *Anacardium humile* populations based on microsatellite loci.

Population	N_A	H_E	H_O	*f*
MON	5.2	0.737	0.703	0.047
COJ	4.7	0.684	0.718	-0.050
MOC	5.0	0.693	0.649	0.065
JAN	5.2	0.727	0.580	0.206*
BAL	5.7	0.725	0.604	0.170*
CAT	5.7	0.713	0.525	0.267*
CLP	5.3	0.714	0.578	0.193*
CAA	5.0	0.687	0.530	0.232*
Over all loci	5.2	0.710	0.611	0.142*

N_A = number of alleles; H_E = expected heterozygosity; H_O = observed heterozygosity; *f* = fixation index.

Values followed by asterisks are significant. For population abbreviations, see legend to Table 1.

The endogamy coefficient (*f*) and the total endogamy coefficient (*F*) were significant when compared to mAoR55, mAoR17, and mAoR52 loci, with the latter two loci having higher values. For the mAoR06, mAoR29, and mAoR46 loci, both the *f* and *F* values were negative. Nevertheless, the mean estimates for *f* (0.139) and *F* (0.203) were significant for the populations (P = 0.0001) (Table 4).

Table 4. Genetic structure of the eight *Anacardium humile* populations.

Locus	*f*	*F*	θ	G_{ST}
mAoR06	-0.035	-0.228	0.037*	0. 033*
mAoR17	0.669*	0.714*	0.136*	0. 123*
mAoR29	-0.035	-0.011	0.024*	0. 021*
mAoR46	-0.207	-0.163	0.036*	0. 032*
mAoR52	0.636*	0.689*	0.147*	0. 131*
mAoR55	0.226*	0.286*	0.078*	0. 069*
Over all loci	0.139*	0.203*	0.075*	0.066*

f = fixation index; *F* = total inbreeding coefficient; θ and G_{ST} = population differentiation.

Values followed by asterisks are significant (P = 0.0001).

Genetic differentiation between populations

The differentiation between the populations was confirmed using the θ and G_{ST} indices, which were significant for all loci (P = 0.0001), with means of 0.075 and 0.066, respectively (Table 4). Values of θ between the pairs of populations revealed significant genetic differentiation among the eight studied populations (Table 5). The BAL and JAN populations were the least differentiated, while the JAN and MOC populations were the most differentiated.

Table 5. Genetic differentiation (above diagonal) and geographical distances (km) (below diagonal) among the eight *Anacardium humile* populations.

	MON	COJ	MOC	JAN	BAL	CAT	CLP	CAA
MON	-	0.067	0.108	0.055	0.056	0.038	0.041	0.057
COJ	230	-	0.081	0.105	0.098	0.059	0.085	0.101
MOC	268	60	-	0.129	0.111	0.094	0.050	0.101
JAN	105	125	166	-	0.025	0.081	0.105	0.060
BAL	114	122	172	31	-	0.052	0.090	0.044
CAT	92	148	197	41	26	-	0.072	0.060
CLP	280	59	22	177	179	205	-	0.059
CAA	223	39	97	122	110	135	92	-

For population abbreviations, see legend to Table 1.

The dendrogram constructed using the UPGMA method based on genetic differentiation (θ) revealed the following hierarchical clustering of genetic differentiation, with two groups and approximately 9% differentiation: [(MON, CAT), ((JAN, BAL), CAA)], [(COJ (MOC, CLP))] (Figure 2).

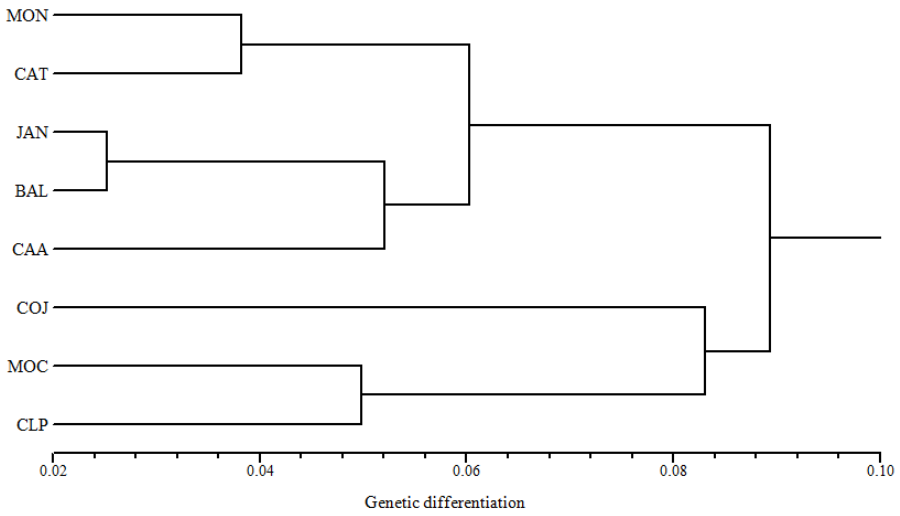

Figure 2. UPGMA dendrogram based on genetic differentiation (θ) among the eight *Anacardium humile* populations. For abbreviations, see legend to Table 1.

The PCA revealed that the first two coordinates explained 59.27% of the variance in the data; coordinate 1 explained 39.72% and coordinate 2 explained 19.55% (Figure 3). The results for the estimates of genetic differentiation (θ) between population pairs (Table 5) corroborated the PCA results. Populations MOC and JAN and MOC and BAL were at opposite ends of coordinate 1. According to the analysis of genetic differentiation between pairs of populations (θ), these pairs exhibited the greatest differentiation at 0.129 and 0.111, respectively.

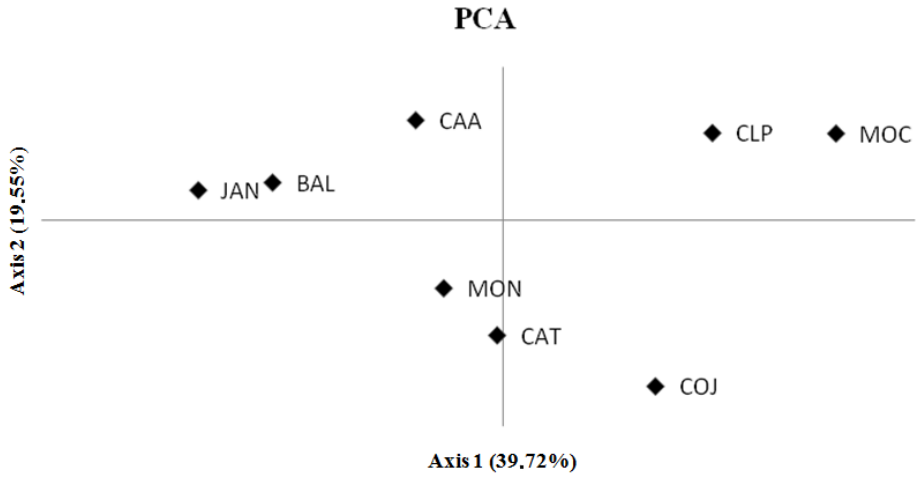

Figure 3. Principal component analysis (PCA) using SSR data among the eight *Anacardium humile* populations. For population abbreviations, see legend to Table 1.

According to the Mantel test, the correlation between genetic and geographical distances for *A. humile* populations was not explained by the hypothesis of isolation by geographical distance ($r = 0.277$, $P = 0.1$).

Spatial genetic structure

Correlogram analysis (Figure 4) revealed a significant SGS for populations MON, JAN, CAT, CLP, and CAA with positive and significant coancestry coefficients ($P < 0.05$). The SGS of the genotypes in the five populations varied among the distance classes from 37 to 231 m in the CLP and MON populations, respectively. Populations MON, JAN, CAT, CLP, and CAA exhibited non-random distributions of genotypes in the first distance classes of 231, 118-185, 98-168, 37, and 50-79 m, respectively. These populations, except for MON, had high endogamy coefficients. In populations with SGS, the f_{ij} decreased at a greater distance. Populations COJ, MOC, and BAL exhibited random distributions of genotypes with non-significant coancestry coefficients. The values of *Sp* revealed strong genetic structuring for most of the populations: MON (*Sp* = 0.072), COJ (*Sp* = 0.006), MOC (*Sp* = 0.028), JAN (*Sp* = 0.064), BAL (*Sp* = 0.030), CAT (*Sp* = 0.095), CLP (*Sp* = 0.076), and CAA (*Sp* = 0.096); the mean for the populations was *Sp* = 0.058.

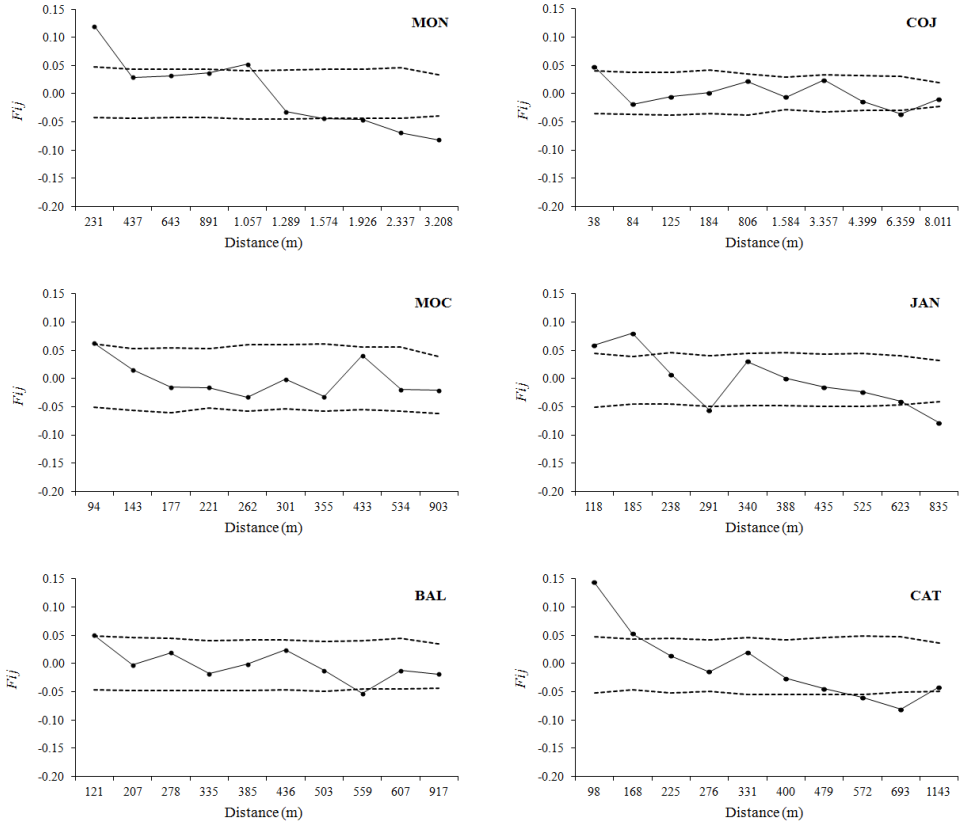

Figure 4. Relationship between kinship (F_{ij}) and distance among the eight *Anacardium humile* populations. Confidence intervals (dashed lines) around each F_{ij} value were obtained through a jackknife procedure over all loci. For population abbreviations, see legend to Table 1.

DISCUSSION

Diversity and genetic structure

The *A. humile* populations analyzed exhibited high genetic diversity, despite positive and significant endogamy coefficients for most populations. The levels of diversity in the *A. humile* populations (H_E = 0.710, H_O = 0.611) are considered high when compared to other native Cerrado species as *Solanum* spp (Moura et al., 2009), *Caryocar brasiliense* (Collevatti et al., 2010), and *Dipteryx alata* (Tarazi et al., 2010).

Considering that anthropic degradation in the Cerrado biome could have affected the levels of genetic diversity in the populations, no direct relationship was found between more degraded populations and low levels of genetic diversity. However, there was a trend for decreasing diversity due to landscape modifications. Populations MOC, CLP, and CAA are among those with the least alleles and lowest H_E values. These populations are also found in the most degraded areas with the greatest devastation to the native plant cover due to the growing of crops and pastures with an extensive reduction in the native flora. Additionally,

population CAA suffered heavy extractivism of fruits by the inhabitants of local communities (Leide Cota personal observations - see Table 1). However, the effects of fragmentation were still not observed in the sampled plants, given that they were adults and must have been established before fragmentation.

Some studies have shown that the damaging effects of accelerated degradation in the Cerrado biome on the structure and genetic diversity of species are not visible because the process is recent (Zucchi et al., 2003; Collevatti et al., 2010). However, it is necessary to analyze other generations, such as juveniles and progeny, to assess the effects of fragmentation on *A. humile*. The implications of fragmentation culminate in the loss of genetic diversity in generations established after fragmentation due to, for example, reduction in the effective population size and changes in the behavior of agents that promote gene flow (Ghazoul, 2005). The wild canids that promote the dispersal of *A. humile* should have promoted allelic exchange between the populations analyzed and thus maintained their levels of genetic diversity.

Genetic differentiation between populations

The genetic relationship between populations, as explained by the axes shown in the PCA graph, does not follow spatial relationship patterns, as geographically close populations are distant from each other on the graph. This finding is confirmed by the Mantel test, which revealed no significant correlation between genetic and geographical distances. Moreover, the estimates of genetic differentiation between populations exhibited the same pattern as the PCA.

The significant genetic differentiation found between *A. humile*, as measured by θ and G_{ST}, suggest a genetic divergence between the populations although the values obtained were low. This result shows that the previous gene flow between populations over time helped make the allelic frequencies similar among them. This finding is supported by the levels of genetic diversity found in the populations and the low percentage of independent alleles in the populations (data not shown).

Estimates of significant genetic differentiation between natural populations have also been found for other plant species in the Cerrado, such as *Eugenia dysenterica* (Zucchi et al., 2003), and *D. alata* (Tarazi et al., 2010). The authors attributed their genetic differentiation to various stochastic processes resulting from isolation by distance, with high gene flow between nearby populations and low gene flow between distant populations. However, such a pattern was not found for the *A. humile* populations. The divergence between the *A. humile* populations analyzed allows for the establishment of a relationship with the high levels of endogamy found, which contributes to the development of the genetic structure. As suggested by Moreira et al. (2009) for populations of *Tabebuia ochracea*, a species that is found in the Cerrado, non-random crossings can contribute to the formation of genetic structure. Similar conclusions could be inferred from the tropical shrub *Erythroxylum havanense* (Domínguez et al., 2005), which has significant levels of genetic isolation between neighboring populations and fine SGS. The levels of genetic differentiation between spatially close *A. humile* populations can also be produced by the presence of the intrapopulational genetic structure.

Spatial genetic structure

The SGS is correlated with the system of crossing, lifestyle, and population density (Bawa, 1979; Vekemans and Hardy, 2004; Geng et al., 2008; Collevatti et al., 2010). Thus,

the development of SGS within *A. humile* populations to form groups of related individuals over short distances could be due to the lifestyle of the species. Individuals of *A. humile* are distributed in various dense spots that show an aggregated spatial pattern (Inofuentes, 2008), forming clusters of available resources. Thus, it is suggested that the SGS in *A. humile* populations results from the local restriction of the area foraged by pollinators as a function of the high availability of resources from few individuals. As reported by Bawa (1979), gene flow in plant species is determined by foraging by dispersal agents and pollinators, which depends on their behavior and the availability of resources distributed over time and space. Nevertheless, the same level of SGS can be obtained for a greater density of resources for dispersal agents and pollinators and smaller dispersal distance, or vice versa. Patterns similar to those suggested for the present study, where the non-random distribution of genotypes is a function of the arrangement of individuals in clusters, were suggested for other plant species, such as *Kandelia candel* (Geng et al., 2008) and *C. brasiliense* (Collevatti et al., 2010).

The non-random crossings resulting from the presence of factors limiting pollen dispersal could have contributed to the high endogamy coefficients found for most of the populations analyzed in the present study, resulting in the intrapopulational genetic structuring in *A. humile* populations. Over the long-term, endogamy is a challenge of panmixia and has various effects that can strongly influence the amount of genetic diversity because high homozygosity reduces the effective population size (Charlesworth, 2003). However, this effect has still not culminated in a marked loss of genetic diversity in the populations studied.

In a study on the successional dynamics of *A. humile* in Cerrado physiognomies, Inofuentes (2008) found that this species was initially established in open physiognomies, continued to develop as the vegetation increased in height and density in closed fields where it reached maximum density, and then decreased in the close Cerrado *sensu stricto*. A similar pattern was observed in the populations analyzed in the present study (Table 1). Based on these observations, it is possible to highlight the tendency for SGS to occur when there is a greater abundance of the species (populations CAT, MON, CAA, and JAN). When the species is less common, the distribution of genotypes trends toward randomness (populations MOC and COJ). Therefore, it has been shown that factors limiting pollen and seed dispersal to short distances exist at locations with greater population density. Based on the results obtained, it is possible that such factors are strictly related to the distribution of the species resulting in the aggregation of resources for agents that promote gene flow. Therefore, the successional dynamics of the species in Cerrado physiognomies contribute to the development of genetic structure in the populations.

Conclusions and implications for conservation

The presence of high genetic diversity in the *A. humile* populations, which reflects the significant genetic variability that still exists in the species, demonstrates the potential for their conservation. Additionally, predatory extractivist exploitation and the anthropic disturbances in the habitats of *A. humile* deserve special attention, as the results show that genetic diversity tends to be lower for populations in more degraded and exploited areas. Appropriated management plans for the extractivist activity must promote the perpetuation of this species and maintenance of its adaptive potential. Therefore, genetic studies on other generations, such as juveniles and progeny, are recommended to assess the effects of fragmentation, permit maintenance of genetic variability, and test for possible genetic differentiation between populations due to frequent and intense modifications to the landscape that reduce the rate at which populations trade alleles.

The SGS observed in most *A. humile* populations demonstrated that the clusters of related plants produced high coancestry coefficients. Besides, the populations exhibiting SGS also had high levels of endogamy that could promote the development of genetic structure in the populations evaluated. The SGS observed in *A. humile* populations is possibly related to the habit and lifestyle of the species, which shows successional dynamics in the different Cerrado physiognomies.

Conflicts of interest

The authors declare no conflict of interest.

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