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Population genetic structure and demographic history of the timber tree *Dicorynia guianensis* in French Guiana

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Abstract

Tropical rainforests host exceptional biodiversity and provide important ecosystem services, but they are facing anthropogenic and climatic threats. Preserving the genetic diversity of forest tree populations is essential for their capacity to adapt and exhibit resilience to environmental changes and anthropic pressures. Here, we collected conservation genetic baseline information for the heavily exploited timber tree *Dicorynia guianensis* Amshoff (Fabaceae) at the regional and local levels in French Guiana. Based on genotyping at five microsatellite loci in 1,266 individuals collected in 23 forest locations, we documented the genetic differentiation of locations from the West and identified distinctive genetic diversity patterns with higher genetic diversity and some bottlenecked sites in the East and inland. The regional population genetic structure is likely

the result of past population isolation in distinct Pleistocene refuges, different demographic histories potentially influenced by Holocene drought periods or palaeofires, and possibly by adaptation to environmental conditions. Assessment of spatial genetic structure (S_p from 0 to 0.028) in five intensively sampled locations yielded estimates of Wright's neighborhood size of 35 - 313, indicative of restricted dispersal and local metapopulation dynamics, and useful as baseline information to assess the effects of selective logging for conservation management. These results support the current management strategies with low impact extraction in three zones of the French Guiana permanent forest domain in *D. guianensis* and allow us to make recommendations for further research and management in order to best preserve its genetic diversity and adaptive potential.

Key words : Tropical tree, Microsatellites, Genetic diversity, Genetic clusters, Timber harvesting, *Dicorynia guianensis*

Introduction

Tropical rainforests are found in wet tropical habitats around the equator, with the largest ones occurring in South America, Western Equatorial Africa, and Southeast Asia. They represent the world's most complex and biodiverse terrestrial ecosystems with a total area estimated at 12 million km² harboring a continuous canopy of tall trees (Gay 2001; Leigh Jr. et al. 2004). There are an estimated 16,000 species of trees in the Amazon lowland rainforest (ter Steege et al. 2013). Rainforests provide many ecosystem services which play a vital role in the survival and quality of life of humans and other species, e.g., the purification of air and water and the mitigation of floods and droughts (Ambe and Onnoghen 2019). Many rainforest regions around the globe are under acute threat of habitat and biodiversity loss because of agricultural development, mining, overexploitation of timber and non-timber forest products, and climate change (Alfaro et al. 2014; Roberts et al. 2017). Genetic diversity within species is paramount to preserve the evolutionary potential of forest tree populations and thus their capacity to adapt and exhibit resilience to environmental changes and anthropic pressures (Sgrò et al. 2011; Alfaro et al. 2014; Hoban et al. 2021a).

Characterizing the genetic diversity and its distribution within and among populations of a species using genetic markers can reveal important baseline information on its conservation status, past population genetic processes, and adaptive potential (Hunter et al. 2021). Genetic diversity is shaped by past demographic and adaptive processes that may have been affected by climatic and/or anthropogenic disturbances (Loveless and Hamrick 1984). In the Amazon basin, the distribution of biota, species, and their genetic diversity is largely attributable to climatic and geomorphological dynamics, with continuous diversification since the late Eocene / early Oligocene (ca. 39 million years before present) and through the Quaternary (Dutech et al. 2003; Rull 2008; Cracraft et al. 2020). The sparse Amazonian palaeoecological record suggests that vegetation changes occurred during glacial and interglacial phases of the Pleistocene with savannah incursions into the forest in northern Amazonia and drought-related fires during the Holocene, especially in the Guiana shield (Charles-Dominique et al. 1998; Bush et al. 2008; Häggi et al. 2017). Palaeoecological and genetic data appear to suggest that Guiana

Shield rainforest communities exhibited widespread resilience to these past disturbances (Dutech et al. 2004; Barthe et al. 2017; Häggi et al. 2017).

The level of genetic diversity relevant for adaptive potential depends on a population's effective population size, N_e , which quantifies the rate of loss of diversity due to genetic drift and inbreeding (Wright 1931). N_e is an important parameter in conservation management and policy as populations with large N_e , especially those with $N_e > 500$, maintain sufficient adaptive potential for long-term persistence and are at reduced risk of maladaptation, genetic erosion, and low fitness (Jamieson and Allendorf 2012). $N_e > 500$ has for example been retained as a genetic indicator to monitor conservation status in the Convention on Biological Diversity's Global Biodiversity Framework (Hoban et al. 2020, 2023). The N_e of plant populations depends strongly on life history traits such as breeding system, reproductive output and seed and pollen dispersal (Schoen and Brown 1991; Wang et al. 2016; Waples 2022). While N_e is suitable to assess conservation status in all species (Hoban et al. 2021b), it is difficult to estimate in species with large numbers of individuals and continuous distributions such as forest trees (Fady and Bozzano 2021; Santos-del-Blanco et al. 2022; Gargiulo et al. 2023).

It has been suggested that in continuously distributed species with large populations, spatial genetic methods that assess the local breeding structure may be more suitable than N_e to monitor conservation status (Neel et al. 2013; Major et al. 2021). The rationale is that in populations where matings preferentially occur between close-by individuals and that thus display isolation by distance, the rate of loss of genetic diversity depends on density and parent-offspring distances. These are conveniently summarized in Wright's neighborhood size NS (Wright 1946; Neel et al. 2013), which is defined as $NS = 4\pi D\sigma^2$, where D is density (number of individuals per unit area) and σ^2 is a measure of dispersal ($\frac{1}{2}$ of the squared axial parent-offspring distance, Wright 1946; Vekemans and Hardy 2004). NS can be interpreted as a number of reproducing individuals in a circle of radius 2σ (assuming Gaussian dispersal, Neel et al. 2013). With wide-ranging dispersal where $D\sigma^2 > 1$, genetic diversity in the total population is lost at a rate of $1/(2N)$, whereas with restricted dispersal where $D\sigma^2 < 1$, the breeding structure slows the loss of genetic diversity in the total population to a rate of $D\sigma^2/(2N)$ (Maruyama 1972; Neel et al. 2013). NS can be estimated from the decline of genetic relatedness with distance, or spatial genetic structure (SGS), as $1/S_p$ (Vekemans and Hardy 2004) and has the potential to serve as a suitable genetic indicator in forest populations where it is more sensitive to management action than N_e (e.g. Piotti et al. 2013; Major et al. 2021). Spatial genetic structure is frequent in tropical forest tree populations with low adult tree densities (Degen et al. 2001; Dutech et al. 2002; Latouche-Hallé et al. 2003; Vekemans and Hardy 2004; Hardy et al. 2006). Through its link with NS , the SGS of tropical tree populations thus provides valuable information on how population density, mating and dispersal, as well as any management actions, affect the maintenance of population genetic diversity relevant for adaptive potential and population resilience (Dick et al. 2008; Piotti et al. 2013; Major et al. 2021).

In French Guiana, timber exploitation and climate change are the greatest threats to tropical rainforest biodiversity (Delnatte and Meyer 2012). In addition, projections for 2050 predict the doubling of the French Guianese human population at a rate of 2.5% of demographic growth per year (INSEE 2019), which will likely result in the development of urban and agricultural areas that will encroach on the rainforest (De Geyer et al. 2020). These events will be accompanied by an increased demand for timber. The Regional Forest and Wood Program of French Guiana (PRFB 2019) aims to produce 210,000 m³/year of certified wood by 2030 compared with an average of 80 000 m³/year between 2009 and 2018 (PRFB 2019; De Geyer et al. 2020), which adds

pressure on already heavily exploited tree species. The first timber species in French Guiana in volume of timber produced is *Dicorynia guianensis* Amshoff (Fabaceae), which represents 55% of timber harvests (Flora 2018). Plastid DNA markers exhibited a moderate genetic structure in *D. guianensis* with $G_{ST}=0.41$ and an East-west gradient of haplotype frequencies along the French Guiana coast attributed to Quaternary forest contraction-expansion dynamics (Caron et al. 2000). The maintenance of high within-population haplotype diversity and weak to moderate SGS with plastid and biparentally inherited markers at the local scale in the Paracou lowland forest was associated with restricted dispersal and the stochastic dynamics and turnover of an aggregated population demographic structure (Latouche-Hallé et al. 2003, 2004). Regional-scale genetic structure at biparentally inherited loci is still unknown in *D. guianensis*, and it is unclear whether local-scale genetic diversity patterns observed in Paracou are specific to this site, or representative of intrapopulation genetic processes in the species. Here, we set out to characterize the regional and fine-scale population genetic structure and genetic diversity of *Dicorynia guianensis* in French Guiana using nuclear genetic markers. Specifically, we addressed the following questions:

- How is *Dicorynia guianensis* structured genetically across French Guiana?

Due to its haploid nature, plastid DNA exhibits 2-4 times stronger drift than nuclear DNA making it suitable to assess recent divergence and colonization patterns within species (Petit et al. 2005; Toews and Brelsford 2012). We thus expect weaker genetic structure at nuclear DNA and hypothesize that any large-scale patterns of genetic structure reliably detected at nuclear markers would be additional evidence for past population isolation. We also hypothesize that populations are locally adapted and that therefore, we can potentially detect an association of population differentiation with environmental drivers. To be interpretable in terms of adaptation, such an association should remain significant when correcting for isolation by distance expected because of local mating events.

- Are there any signals of past demographic events such as bottlenecks?

Nuclear markers will allow us to test reliably for recent demographic bottlenecks and potentially provide more solid evidence for population demographic history.

- To what extent is SGS variable among sites and to what extent does it inform us on intrapopulation processes relevant for conservation management?

Dicorynia guianensis is distributed in aggregates and exhibits variable density within forest locations. We hypothesize that the strength of SGS within populations will consequently vary among sites and provide a view on the variability of local populations regarding parent-offspring distances and the rate of local loss of genetic diversity relevant for conservation.

Our study will enhance our knowledge on the demographic history and ongoing population genetic processes in *D. guianensis*, which is valuable baseline information for the future study of adaptive genomic variation and its drivers, and the design of sustainable management recommendations.

Material and Methods

Study species

Dicorynia guianensis, commonly named Angelique, is an ecologically and economically important endemic tree species of the Guiana shield which represents 55% of the timber production of French Guiana, with main uses in carpentry, joinery, flooring, and harbor works (Flora 2018). This drought sensitive species (Maréchaux et al. 2015) is the 16th hyperdominant species in terms of productivity and biomass of wood in the Amazon basin, even if its distribution area covers only the Guiana Shield (Fauset et al. 2015). Studies in the coastal lowland forest of the Paracou research station in French Guiana report that *D. guianensis* is distributed in aggregates of about 0.4 ha, with an average density of 6.9 mature trees per ha (Bariteau 1993; Gourlet-Fleury et al. 2004). Aggregates are genetically differentiated (Caron et al. 1998; Latouche-Hallé et al. 2003), which can be explained by a rather short average seed dispersal distance (30 m; 5% beyond 50 m) ensured by gravity and wind (Jésel 2005). Pollination in this predominantly outcrossing species is provided by large bees, ensuring pollen flow over an average distance of 200 m around the source tree in the Paracou research station (Caron et al. 1998; Forget et al. 2001). Regeneration in *D. guianensis* is strongly dependent on the opening of forest gaps and population dynamics of the aggregates are believed to follow a rapid extinction–recolonization turnover (Caron et al. 2000). Colonization efficiencies vary between locations, ranging from simple aggregates in Paracou to patches covering several hectares in Regina (Guitet et al. 2014).

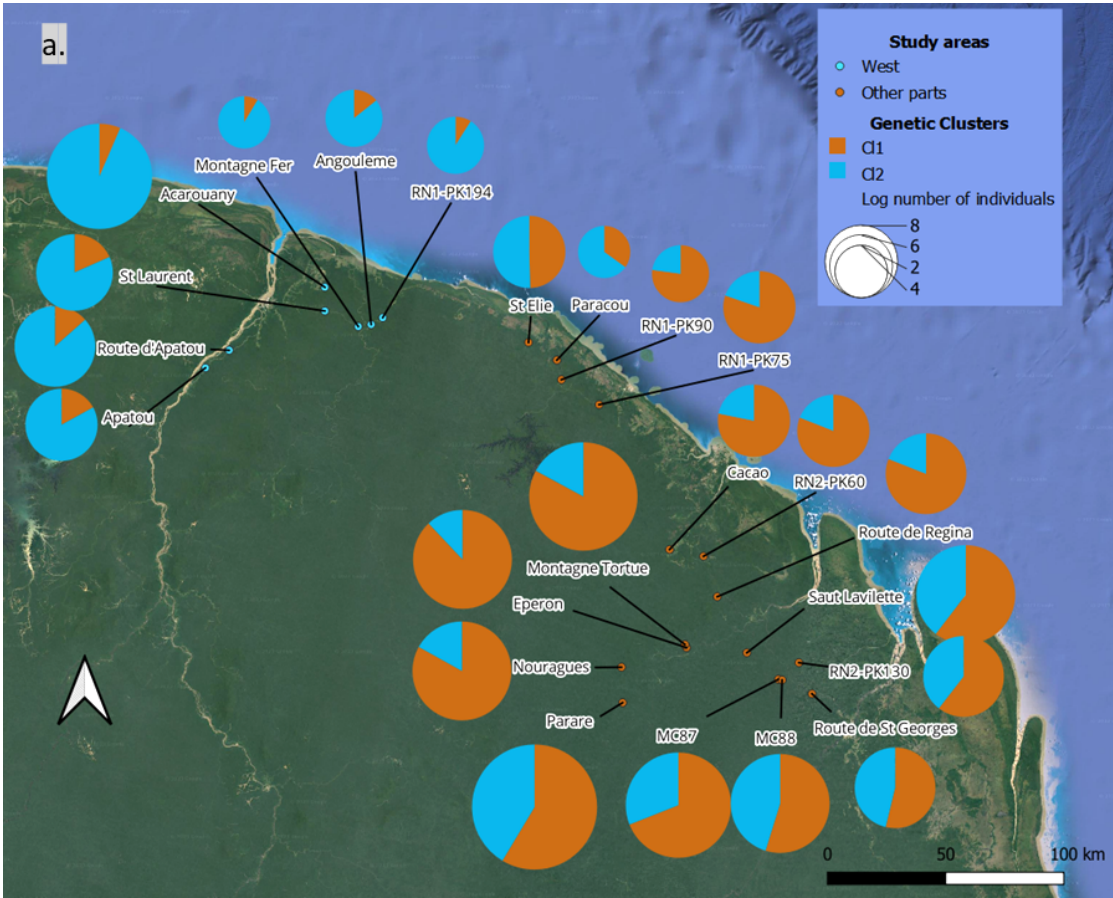
Sampling and genetic data

We used three SSR (simple sequence repeat, or microsatellite) data sets (DS1, DS2, DS3) on the same five SSR loci (Latouche-Hallé et al. 2003) in *Dicorynia guianensis* to explore the research questions exposed above in French Guiana. The protocol for DNA extraction, SSR amplification and genotyping is described in Supplementary Material S1. DS1 and DS3 were generated for this study, DS2 was reanalysed from Latouche-Hallé et al. (2003). DS1 comprised n=647 trees sampled in 23 locations across French Guiana (Table 1, Figure 1) and was used to assess regional-scale genetic structure and fine-scale spatial genetic structure in two locations (Acarouany and Eperon). The majority of sampling locations represent coastal lowland forests. DS2 comprised n=117 trees sampled to assess fine-scale spatial genetic structure in the Paracou research station. DS3 comprised n=502 trees from Regina and n=300 trees from Nouragues Grand Plateau sampled to assess fine-scale spatial genetic structure. The five locations (Acarouany and Éperon from DS1, Paracou from DS2, Regina and Nouragues from DS3) used to study the spatial genetic structure had sample sizes of a minimum of 48 georeferenced individuals. Individuals sampled had a diameter at breast height (dbh) of > 10 cm, except in Nouragues Grand Plateau, where individuals with dbh < 10 cm were also sampled. Tree densities within locations were recorded as the average number of individuals with ≥ 30 cm dbh / ha based on surveys of ≥ 30 ha of forest to provide comparable averages accounting for the aggregated local distribution of the species.

Table 1. Genetic diversity and population demographic history statistics for 23 study sites of *Dicorynia guianensis* based on dataset DS1. N , sample size; A_R allelic richness standardized to a sample size of 10 gene copies; NP mean number of private alleles per locus; pA_R private allelic richness for a standardized sample of 10 gene copies; H_E , expected heterozygosity; H_O , observed heterozygosity; F_{IS} , inbreeding coefficient; P -value ($F_{IS} < 0$) after 1,000 randomization of gene copies among individuals; T_2 , bottleneck statistic and significance of the bottleneck test that examines if the proportion of loci with excess heterozygosity is significantly greater than that expected under the infinite alleles model (IAM); M ratio; statistic that evaluates ancient bottlenecks, and its significance. *ns*, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. NA, not available.

Study sites	N	A_R	NP	pA_R	H_E	H_O	F_{IS}	T_2 (IAM)	M ratio
Acarouany	48	3.47	0	0.70	0.568	0.529	0.070	0.484	0.447
Route Apatou	9	3.38	0	NA	0.602	0.543	0.111	NA	0.354
Apatou	6	NA	0.2	NA	0.618	0.587	0.071	NA	0.358
St Laurent	8	NA	0.2	NA	0.609	0.664	-0.101	NA	0.466
Angoulême	3	NA	0	NA	NA	NA	NA	NA	0.587
Montagne Fer	2	NA	0	NA	0.433	0.500	-0.500	NA	0.211
RN1-PK194	3	NA	0	NA	0.620	0.500	0.268	NA	0.449
Overall West	79	3.43	0.06	0.70	0.575	0.554	-0.014	NA	NA
Paracou	1	NA	0	NA	NA	NA	NA	NA	0.577
St Elie	6	NA	0	NA	0.634	0.620	0.026	NA	0.278
Montagne Tortue	29	3.22	0.2	0.17	0.595	0.540	0.094	0.383	0.343
Eperon	57	3.14	0.2	0.16	0.559	0.466	0.168***	0.488	0.308
Route de Regina	9	NA	0	NA	0.718	0.782	-0.122	NA	0.305
RN2-PK60	6	NA	0	NA	0.720	0.600	0.180	NA	0.292
Cacao	6	NA	0	NA	0.639	0.650	-0.010	NA	0.388
RN1-PK75	6	NA	0	NA	0.555	0.620	-0.134	NA	0.253
RN1-PK90	3	NA	0	NA	NA	NA	NA	NA	0.186
Pararé	280	3.87	2.4	0.32	0.677	0.632	0.066***	2.107*	0.378
Nouragues	33	3.12	0	0.09	0.528	0.552	-0.047	0.350	0.292
Saut Lavilette	30	3.56	0.4	0.26	0.627	0.565	0.101	1.451	0.265
MC87	30	4.12	0.4	0.33	0.700	0.607	0.135	2.040*	0.290

MC88	52	3.87	0.4	0.19	0.709	0.760	-0.072**	2.138*	0.322
Route de St Georges	9	NA	0	NA	NA	NA	NA	NA	0.402
RN2-PK130	11	NA	1.6	NA	0.729	0.770	-0.085	NA	0.325
Overall other sites	568	3.56	0.35	0.22	0.645	0.628	0.023	NA	NA
Overall	647	4.08	0.26	0.28	0.696	0.610	0.012	NA	0.351



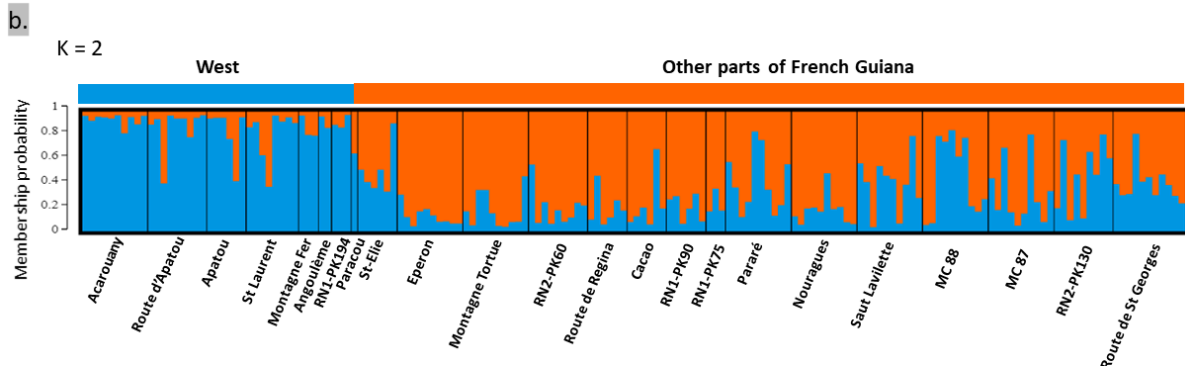


Figure 1. Genetic structure of *Dicorynia guianensis* in French Guiana. a. Geographical genetic structure of the 23 sampling locations of dataset DS1 subsampled to a maximum of 10 individuals per location; the size of pie charts is proportional to the logarithm of the number of individuals sampled in each location. b. Bayesian estimates of population structure based on SSR data in sampling locations. Each vertical line represents one individual and color segments represent its assignment proportions to each of $K=2$ genetic clusters.

Data analysis

Assessment of allelic diversity and genotyping quality

The number of alleles at each locus was assessed in DS1 using the software SPAGeDi 1.5 (Hardy and Vekemans 2002). Genotyping problems such as null alleles, PCR artifacts caused by large allele drop-out, or stuttering were assessed with MICRO-CHECKER 2.2.3 (Van Oosterhout et al. 2004). The presence of null alleles was assessed in each sampling location ($n > 20$, DS1, DS2, and DS3). The estimated null allele frequency for each locus was calculated using the methods of Chakraborty and colleagues (Chakraborty et al. 1992) and Brookfield (Brookfield 1996). The R package *poppr* (Kamvar et al. 2014) was used to detect replicated identical genotypes (e.g., due to cross-sample contamination or clonality).

Genetic structure and differentiation

A Bayesian clustering approach was applied to DS1 using STRUCTURE 2.3.4 (Pritchard et al. 2000) to detect population genetic structure and estimate the number of distinct genetic clusters (K) across French Guiana. To reduce bias into the identification of genetic discontinuities in STRUCTURE caused by geographically uneven sampling (Puechmaille 2016), we used 10 randomly selected individuals per site for the sites with $n > 10$ and all available individuals in the sites with $n \leq 10$. The analyses were conducted under the admixture model with correlated allele frequencies among populations. We ran ten repetitions for each assumed number of clusters K , with $K=1$ to $K=15$, using a burn-in length of 50,000 and a run length of 500,000 MCMC steps. Results were summarized with STRUCTURE Harvester version 0.6.94 (Earl and vonHoldt 2012) and the Clumpak server (Kopelman et al. 2015). To determine the K that best described the structure of the data, we used the log posterior likelihood of the runs plotted against K and the delta K approach (Evanno et al. 2005), in conjunction with individual assignment proportions. Assignment proportions of individuals were graphically represented as histograms using Structure Plot V2.0 (Ramasamy et al. 2014). Pie charts displaying average assignment proportions per location were mapped on the 23 sampling locations and edited in QGIS 3.16.3

(Quantum GIS Development Team, <http://qgis.osgeo.org>). The subsampled dataset of a maximum of 10 individuals per site was also used to assess geographical genetic structure in a Bayesian Analysis of Population Structure with spatial prior information implemented the program BAPS ver. 5.3 (Corander et al. 2008) and to perform a discriminant analysis of principal components (DAPC) with the ADEGENET package v. 2.1.8 in R (Jombart 2008).

Using SPAGeDi 1.5 (Hardy and Vekemans 2002), we obtained estimates of genetic differentiation between the 23 study sites and overall differentiation between populations. Estimates were obtained a) from all individuals at the 23 sites, b) from the subsampled dataset with a maximum of 10 individuals per site and c) using only sites containing 10 or more individuals (i.e. 10 sites). We used the pairwise F_{ST} (Weir and Cockerham 1984), which ignores information on allele size, and obtained confidence intervals (95%) from permutation tests of individuals among populations (10,000 permutations). We also assessed genetic differentiation using R_{ST} and evaluated the contribution of allele size variation to genetic differentiation using 10,000 permutations of allele sizes among alleles. The result was used to select the most appropriate SSR mutation model, i.e. the infinite allele model if allele sizes do not contribute to differentiation, or alternatively, a stepwise mutation model or a two-phase model, for the analysis of population demographic history (Cornuet and Luikart 1996; Piry et al. 1999).

We additionally conducted analyses of Molecular Variance (AMOVAs) to assess the geographic partitioning of genetic diversity using Arlequin (Excoffier and Lischer 2010). To assess the effect of genetic drift on genetic differentiation, isolation by distance analyses were done by regressing $F_{ST}/(1-F_{ST})$ on the logarithm of spatial distance with SPAGeDi 1.5 (Hardy and Vekemans 2002) and testing for significance by permuting individuals among populations (10,000 permutations). To assess whether environmental variables had a stronger effect than isolation by distance on differentiation among locations, we conducted simple and partial Mantel tests (controlling for geographical distance) using the vegan package (Dixon 2003) in R. As environmental variables, we used 1) annual rainfall extracted from the WorldClim database (Fick and Hijmans 2017), computing the absolute distance in annual rainfall for pairs of sites; and 2) an integrative spatialized categorical variable, the “forest habitat” (Guitet et al. 2015a) for which we established a binary distance matrix with “1” for shared forest habitat and “0” for different habitats. Sampling sites were located in five forest habitats: irregular hill forest, mid-mountain forest, lowland valley forest, high plateau forest, and coastal rock forest. Simple Mantel tests were performed to assess the correlation between the genetic distance matrix and each of the environmental distance matrices. For partial tests, we assessed the same correlations correcting for geographic distance. All tests used Pearson's correlation coefficient, with significance tested by 10,000 permutations. These variables were chosen because rainfall exhibits a marked gradient across French Guiana with the highest values in the East, and because forest habitat integrates topographical and geomorphological features that have affected the forest history and because it is relevant for timber extraction.

Genetic diversity, inbreeding, and population demographic history

Using SPAGeDi 1.5 we recorded the allelic richness A_R , the mean number of private alleles per locus NP , the expected and observed heterozygosities (H_E and H_O), and the inbreeding coefficient (F_{IS}). The

significance of F_{IS} was assessed with randomization tests of gene copies among individuals (1,000 permutations). In addition we computed the private allelic richness pA_R with ADZE (Szpiech et al. 2008), using a rarefaction approach to measure the number of distinct alleles private to sampling sites.

Demographic processes such as recent bottlenecks transiently produce a greater decrease in allelic richness than in genetic diversity: as a consequence, an excess of genetic diversity (H_E) can be observed in recently bottlenecked populations, relative to expectations under drift-migration equilibrium (i.e., constant population size). We used the BOTTLENECK software to calculate the T_2 statistic which determines if the proportion of loci with heterozygosity excess is significantly larger than expected at equilibrium (Cornuet and Luikart 1996; Piry et al. 1999). This analysis was conducted with the Infinite Alleles Model (IAM, determined to be the most appropriate model for the data, see Results). We also computed the M ratio, an index appropriate to identify more ancient bottlenecks, which represents the relationship between the number of alleles k , the distance between these alleles, and the overall range of allele size (Garza and Williamson 2001). Under genetic drift, rare alleles are more likely to be lost which decreases the total number of alleles without necessarily decreasing the allele size range. The M ratio and its significance were assessed using Arlequin 3.5 (Excoffier and Lischer 2010).

Fine-scale spatial genetic structure

Fine scale spatial genetic structure (SGS) analyses were conducted in a total of five locations with $n \geq 48$ samples from DS1 and in the locations from DS2 and DS3: Acarouany, Eperon, Nouragues Grand Plateau (two dbh classes: below and above 10 cm), Paracou, and Regina. Pairwise kinship coefficients F_{ij} (Loiselle et al. 1995) were computed with SPAGeDi 1.5a and plotted against the logarithm of geographic distance between individuals using six predefined distance classes with upper bounds of 40, 80, 160, 320, 640, and 1280 m such that the proportion (%) of all individuals represented at least once in the distance classes (% partic) was ≥ 50 . The average kinship coefficient F_1 of the first distance class was considered as the estimate of kinship within aggregates. Significance of SGS was assessed as the deviation from random expectations of the regression slope b of F_{ij} on the logarithm of distance, using 10,000 permutations of individual locations. The strength of SGS was quantified with the Sp statistic, $Sp = -b/(1 - F_1)$, following Vekemans and Hardy (2004) and Wright's neighborhood size NS was computed as $1/Sp$, to provide an estimate of the local breeding structure related to the effective population size N_e (Wright 1943) that can serve as baseline information on local genetic diversity for conservation as suggested by Major et al. (2021). To estimate local gene dispersal σ , where σ^2 is half the average squared axial parent-offspring distance, we used the iterative procedure proposed in Vekemans and Hardy (2004), using as effective density De 0.1 times the observed location density D of individuals with dbh > 30 cm. The ratio $De/D = 0.1$ is a conservative estimate for effective density (Hardy and Vekemans 1999) analogous to the ratio $Ne/N=0.1$ proposed to estimate Ne from the census size (Hoban et al. 2020; Laikre et al. 2021). We also assessed whether there was an effect of population density on SGS by regressing Sp on density across locations. The spatial genetic structure of the five locations was also studied using spatial principal component analysis, sPCA, based on a Delaunay triangulation as a connection network in ADEGENET v.2.1.8 in R (Jombart 2008). The strength of the spatial genetic structure was estimated by the eigenvalue of the first sPCA axis. We tested for global and local spatial genetic structure, using the G-test and L-test respectively.

Results

Genotyping quality

The number of alleles per locus ranged from five to 15, for a total of 46 alleles over the five loci in DS1. No genotyping problems were found in any of the data sets and the *poppr* analysis did not identify any replicated genotypes among individuals, indicating absence of clonal propagation or sample cross-contamination in the laboratory.

Genetic structure

STRUCTURE analysis identified $K=3$ as the best clustering solution in DS1 subsampled to a maximum of 10 individuals per site based on delta K and on the log posterior likelihood (Supplementary file, Figure S1). With $K=3$, high assignment proportions, e.g. $q \geq 90\%$, were only observed in a single genetic cluster whereas many individuals were admixed with similar assignment proportions in the other two clusters (Figure S2). Following recommendations of the STRUCTURE documentation, we report results for $K=2$, the smallest value of K that captures the major structure in the data (Figure 1). Average assignment proportions per sampling location (Figure 1a) illustrated the genetic distinctiveness of sites located in the West vs. those in the rest of French Guiana. BAPS (Supplementary file, Figure S3) and DAPC (Supplementary file, Figure S4) analyses were broadly congruent with those from STRUCTURE, with DAPC confirming the genetic distinctiveness of West plots along PC1 (represented by blue circles in the graph, Figure S4). Pairwise F_{ST} values confirmed this major regional pattern of population genetic structure (Tables S1, S2), e.g. when considering sites with $n \geq 10$, the western site (Acarouany) displayed pairwise F_{ST} values from 0.095 to 0.236 (Table 2) whereas F_{ST} among sites in the rest of French Guiana ranged from 0.015 to 0.182 (Table 2). Sites in the West appeared genetically homogeneous with no significant pairwise F_{ST} detected although this might be an effect of low sample size, see analyses with the complete and the subsampled datasets (Table S1, Table S2). Some sites in the rest of French Guiana, e.g. Pararé inland and RN2-PK130 in the East also displayed elevated pairwise F_{ST} values. Overall differentiation among sampling sites was significant with $F_{ST} = 0.094$, ($P < 0.001$) and with $R_{ST} = 0.040$ ($P < 0.001$). R_{ST} was not larger than its mean value based on permutation of allele sizes, indicating that SSR allele size mutations did not increase genetic differentiation. Based on this result, we selected the infinite alleles model (IAM) as the most suitable mutation model for the analyses of population demographic history.

Variance partitioning with AMOVA in DS1 showed that a regional division of West vs. rest of French Guiana accounted for 7% ($F_{CT}=0.070$, $P < 0.001$) and differentiation of sites within regions for 3% ($F_{SC}=0.034$, $P < 0.001$) of the genetic variation, while most of the variation resided within individuals (Supplementary file, Table S3). Genetic isolation by distance was observed in DS1 in French Guiana ($R^2 = 0.0659$, $P < 0.05$) but not in the group of western sites ($R^2 = 0.0406$, $P > 0.05$) or among all other sites ($R^2 = 10^{-5}$, $P > 0.05$) (Supplementary file, Figures S5, S6). The Mantel test assessing the association between genetic distance and forest habitat was not significant, however, genetic distance was significantly associated with annual rainfall ($R^2 = 0.155$, $P < 0.05$) but the association did not remain significant when controlling for geographic distance.

Table 2. Pairwise F_{ST} values between study sites with 10 or more individuals of *Dicorynia guianensis*. Significance of values is based on permutation tests of individuals between pairs of populations (10,000 permutations): *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Study areas		West	Other parts of French Guiana								
	Study sites	Acarouany	Eperon	MC87	MC88	Montagne Tortue	Saut Lavilette	Pararé	Nouragues	Route de St Georges	RN2-PK130
West	Acarouany	-	0.181***	0.095***	0.134***	0.197** *	0.126** **	0.134** *	0.141***	0.227***	0.236***
Other parts of French Guiana	Eperon		-	0.083***	0.096***	0.016	0.123** **	0.112** *	0.094***	0.016	0.115***
	MC87			-	0.015*	0.074** *	0.026* *	0.108** *	0.069***	0.048*	0.061**
	MC88				-	0.066** *	0.069* **	0.139** *	0.084***	0.114***	0.089***
	Montagne Tortue					-	0.132* **	0.160** *	0.126***	0.056	0.119***
	Saut Lavilette						-	0.064** *	0.062***	0.024	0.073***
	Pararé							-	0.050***	0.103**	0.182***
	Nouragues								-	0.094***	0.117***
	St Georges									-	0.056

Genetic diversity and inbreeding

Expected heterozygosity varied from $H_e=0.433$ (Montagne Fer) to $H_e=0.729$ (RN2-PK130) (Table 1), exhibiting an increasing West-East genetic diversity trend, illustrated for example by the intensively sampled locations with $H_e=0.568$ in Acarouany (West) and $H_e=0.690$ in Nouragues Grand Plateau (inland, Table 3). The allelic richness for a standardized sample size of 10 gene copies followed a similar trend with lower values in the West (average $A_R=3.43$) than in the other sites (average $A_R=3.56$, Table 1). Conversely, private allelic richness was higher in the West with $pA_R=0.70$ than in other sites, $pA_R=0.22$ (Table 1). The mean number of private alleles varied from 0 for most sampling sites to $NP=2.4$ (Pararé). Significant inbreeding, as estimated by F_{IS} , was detected in only three sampling locations (DS1, Table 1) and in three out of five intensively sampled locations (Table 3). In Nouragues Grand Plateau, individuals with dbh < 10 cm were more inbred ($F_{IS} = 0.120$) than the larger individuals ($F_{IS} = 0.050$) (Table 3). The T_2 values obtained in BOTTLENECK were unaffected by sample size (results not shown). They were consistent with mutation-drift equilibrium in most sites and revealed a

heterozygosity excess indicative of a recent bottleneck in three inland sampling sites (MC87, MC88, and Pararé) in DS1 (Table 1) and in two intensively sampled locations, the Nouragues Grand Plateau in the same inland region and the eastern location of Regina (DS3, Table 3). The *M ratio* test which typically detects ancient bottlenecks was non-significant in all sampling sites (Table 1, Table 3).

Fine-scale spatial genetic structure

Significant spatial genetic structure was detected in Paracou, Regina, and both diameter classes of Nouragues Grand Plateau, but not in Acarouany nor in Eperon, with *Sp* ranging from -0.0057 (Acarouany) to 0.0286 (Paracou) (Table 3, Figure 2). There was no difference in SGS between diameter classes in Nouragues Grand Plateau (Table 3). Estimates of Wright's neighborhood size ranged from 35 to 313 and could not be calculated in Acarouany (Table 3). The iterative procedure to estimate gene dispersal sigma converged in a single location only, in Regina where $\sigma = 156$ m. We observed a negative relationship between stand density and *Sp*: forest locations with higher density had lower *Sp* ($R^2=0.32$), suggesting an increased overlap of gene dispersal shadows. Spatial principal component analysis, sPCA, detected global spatial genetic structures by means of a significant G-test in the three locations with significant *Sp*, Paracou, Regina, and Nouragues Grand Plateau, suggesting spatial autocorrelation, whereas L-tests for genetic differentiation of neighboring individuals were non-significant in all locations (Supplementary Figure S7). Patterns of spatial autocorrelation were observable based on the spatial interpolation of individual scores on the first global sPCA axis (Supplementary Figure S8).

Table 3. Genetic diversity, fine-scale spatial genetic structure and population demographic history statistics in five locations of *D. guianensis* in French Guiana. *N*, number of individuals sampled; *Ind/ha*, number of individuals per hectare (dbh>30cm); σ , estimate of gene dispersal (half the mean square parent-offspring distance); H_E , expected heterozygosity; F_{IS} , inbreeding coefficient; F_{ij} , average pairwise kinship coefficient in the first distance class, up to 40m; %partic, the proportion (%) of all individuals represented at least once in the first distance class; b-log, slope of the regression of F_{ij} on the logarithm of distance; *Sp* statistic to quantify the strength of SGS along with its significance; *NS*, Wright's neighborhood size; *T2* bottleneck statistic and significance of the bottleneck test that examines if the proportion of loci with excess heterozygosity is significantly greater than that expected under the infinite alleles model (IAM); *M ratio*; statistic that evaluates ancient bottlenecks, and its significance. *ns*, not significant; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$. *NA*, Not applicable, the bottleneck test is not applicable to trees below 10 cm dbh. *n.c.*, no convergence for gene dispersal estimate.

Locations	Data Set	<i>N</i>	<i>Ind/ha</i>	σ	H_E	F_{IS}	F_{ij} (1 st class)	% partic	b-log	<i>Sp</i> statistic	<i>NS</i>	<i>T2</i>	<i>M ratio</i>
Acarouany	DS1	48	7.2	n.c	0.568	0.070 ns	0.011	97.9	0.006	-0.0057ns	-	0.484	0.447
Eperon	DS1	56	NA	NA	0.561	0.164** *	0.095	50.0	-0.003	0.0032ns	312.5	0.488	0.308
Paracou	DS2	117	2.5	n.c	0.609	0.013 ns	0.091	88.9	-0.026	0.0286***	35.0	1.272	0.448

Regina	DS3	502	12.5	156	0.675	0.094** *	0.053	99.6	-0.008	0.0086***	116.3	2.025*	0.324
Nouragues Grand Plateau (dbh < 10cm)	DS3	93	NA	NA	0.625	0.120** *	0.036	98.9	-0.014	0.0150**	66.7	NA	NA
Nouragues Grand Plateau (dbh ≥ 10cm)	DS3	207	5.0	n.c	0.690	0.050**	0.049	97.1	-0.014	0.0151***	66.2	2.090*	0.378

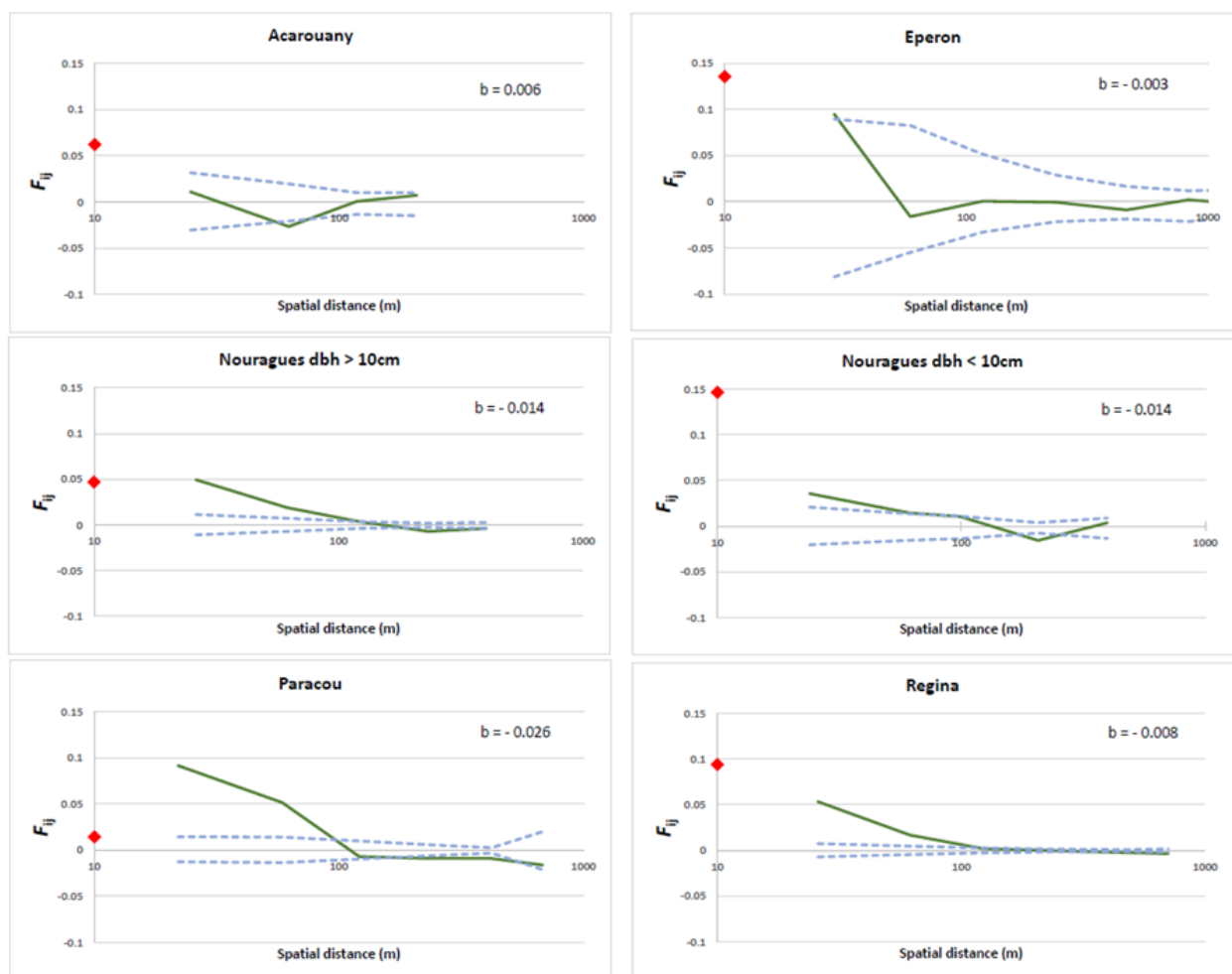


Figure 2. Spatial autocorrelogram of the kinship coefficient (F_{ij}) as a function of the spatial distance. The dashed lines correspond to the upper and lower limits of the 95 % confidence interval for spatial randomness of genotypes, constructed by 10,000 permutations of individual locations among all individuals. The slope of the regression of kinship on log(dist) is indicated as b for each correlogram. Significant spatial genetic structure was

detected in both diameter classes in Nouragues, in Paracou, and in Regina. The red rhombus represents the intra individual values of the kinship coefficient.

Discussion

Dicorynia guianensis population structure and demographic history

We discerned regional population genetic structure in *Dicorynia guianensis* based on SSR data in French Guiana. The western locations sampled in our study displayed distinctive private alleles but were less diverse than locations in central or eastern French Guiana. Pairwise differentiation analysis suggested additional patterns of genetic structure among some locations in inland or eastern French Guiana but these were not robustly identified from our data with multiple methods. Population genetic structure with distinct genetic clusters including east-west divergence was also observed in other rainforest trees in French Guiana, e.g., in *Vouacapoua americana* (Dutech et al. 2003), *Carapa surinamensis*, and *Carapa guianensis* (Barthe et al. 2017) where it was attributed to past population isolation. We observed a pattern of isolation by distance in our data, suggesting a role of genetic drift due to spatially restricted dispersal. Genetic differentiation was also associated with annual rainfall, but this association did not persist when controlling for geographic distance, suggesting that past population isolation and restricted dispersal (see below) are sufficient to explain the genetic structure in our data. The annual rainfall in French Guiana is highest in the east and declines towards the west, where the dry season is more pronounced, and towards the south (inland) (Wagner 2011), and is thus correlated with spatial distance. Future studies can assess the effects of French Guiana's wealth of complex abiotic conditions and gradients (Guitet et al. 2015b) as drivers of selection at the genomic level in *D. guianensis* (Brousseau et al. 2015, 2021).

In *D. guianensis* plastid DNA displayed an East-west and a Center-inland trend of differentiation and a moderate genetic differentiation of $G_{ST}=0.41$ among locations, indicating restricted gene flow by seed, especially along a south-west to north-east axis (Caron et al. 2000). Our SSRs similarly suggested limited gene flow between Western and other locations along the French Guiana coast. However, the SSR differentiation between western and inland populations was not captured by plastid DNA, and comparison of differentiation patterns was not possible for the extreme eastern populations that remained unsampled in Caron et al. (2000). The stronger structure of plastid markers ($G_{ST}=0.41$ for plastid DNA vs. $F_{ST}=0.09$ for nuclear markers) at the regional scale was congruent with stronger pollen-mediated than seed-mediated gene flow in *D. guianensis* already described at the local scale (Caron et al. 2000; Latouche-Hallé et al. 2004). Past population isolation in refugia during the dry Pleistocene glacial periods and subsequent recolonisation in response to Pleistocene and Holocene climate oscillations likely contributed to shaping the observed population genetic structure (De Granville 1982; Tardy 1998). Several rivers in French Guiana may have contributed as well, for example acting as barriers to seed and pollen dispersal as has been observed for other Amazonian woody species (Nazareno et al. 2017, 2021). Refugia where tree populations likely persisted during the dry glacial periods have been suggested in the Guiana Shield, including in Suriname (Fouquet et al. 2012; Alonso and Berrenstein 2022) and

French Guiana (De Granville 1982). Considering that *D. guianensis* is present west of French Guiana, the distinctiveness of western sites detected in our study could thus have been influenced by refugia located in Suriname (Bush 1994; Fouquet et al. 2012). In French Guiana, Pleistocene forest refugia were suggested in upland locations in the eastern coastal region and in the central inland Massif Central Guyanais (De Granville 1982; Guitet et al. 2015b). Significant differentiation in *D. guianensis* in the large area comprising coastal, central and inland sampling sites and the detection of bottlenecks in some of them suggest heterogeneous population demographic histories in this geologically complex region. In particular, paleoecological studies based on charcoal analyses showed that the areas of lower altitude in Plateau des Nouragues had been disturbed during the Holocene (10k – 1k years ago) as a potential consequence of natural fire events during the driest periods. One possible hypothesis is thus that the tree populations present in Plateau des Nouragues have suffered bottlenecks (Table 1, Table 3) due to such palaeofires. Nearby swampy lowlands may have played a demographic buffering role for *D. guianensis* populations of the Plateau des Nouragues (Charles-Dominique et al. 1998). It is, however, difficult to precisely identify the origin of bottleneck signals in other sites where they were detected, such as in Regina. The present population in Regina could have migrated from areas affected by palaeofires, or it may have been affected by other factors. The available data does not allow us to distinguish among these hypotheses. The glacial exposure of offshore areas and a Holocene marine transgression (6,000 BP) may additionally have contributed to shaping population demographic history of trees in the coastal plain (Tardy 1998; Bongers et al. 2001).

To distinguish the effects of the mentioned putative drivers of population genetic structure in *D. guianensis*, future studies should collect genomic data to examine genomic signatures of selection by putative environmental drivers and to obtain a better resolution in the reconstruction of population demographic history. Such studies should also examine processes that differentially affect maternally inherited plastid DNA markers vs. biparentally inherited nuclear markers.

Fine-scale spatial genetic structure

Spatial genetic structure within plant populations is determined by species' life history traits, foremost the mating system and dispersal syndromes. In *D. guianensis* a mostly outcrossing mating system favors gene flow, whereas seed dispersal by gravity and wind results in short dispersal distances (Caron et al. 1998). The SGS observed in *D. guianensis* locations (mean S_p of 0.011) is weak to moderate in comparison with other plant species (S_p ranging from 0.0003 to 0.2632, Vekemans and Hardy 2004) and similar to that of other tropical tree species of the region, like *Carapa guianensis* (Cloutier et al. 2007), *Symphonia globulifera* (Degen et al. 2004), and *Sextonia rubra* (Hardy et al. 2006). Significant SGS was observed in three out of five locations and individuals in aggregates were more related than expected by chance in four locations (F_{ij} of the first distance class, spatial representation of sPCA scores, Figure S8). These results suggest a maintenance of local genetic structure through occasional selfing (about 15%, Caron et al. 1998), some biparental inbreeding (mating between relatives, e.g., in Paracou where F_{ij} was higher than F_{is}) and overall restricted seed dispersal. The observation of stronger SGS in the plot with the lowest density (Paracou), and more generally the negative correlation between density and S_p , supports the seed shadows hypothesis, which posits that higher density results in overlap of seed shadows, and thus weaker SGS (Jordano and Godoy 2002). The population dynamics

of *D. guianensis* has been proposed to strongly depend on the opening of forest gaps that allow for the establishment of new aggregates (Caron et al. 2000). A hypothesis is that such openings may be colonized thanks to occasional secondary seed dispersal by rodents. The variation in rodent disperser populations is strongly impacted by hunting in coastal areas near logging areas in French Guiana (Johns 1988; Beckman and Muller-Landau 2007; Dirzo et al. 2007), which may have effects on SGS (stronger in intensively hunted areas) and the colonization dynamics of the species. In the locations with the smallest sample sizes Acarouany ($n = 48$) and Eperon ($n = 56$), SGS was not significant, possibly suggesting a lack of power of the data sets. According to Cavers et al. (2005), if the SGS of a species is expected to be weak, sample size should be greater than 100 for efficient SGS estimations. The number of genetic markers is also important; e.g., hundreds of SNP markers provided better estimates of S_p than nine SSR markers in the pine species *P. halepensis* which also shows weak SGS (Budde et al. 2017).

We would a priori expect a decrease in SGS between life stages from seedlings to adults due to demographic thinning (Chung et al. 2003). In our study we did not observe any difference in S_p between individuals from Nouragues Grand Plateau with $dbh > 10$ cm and those with $dbh < 10$ cm. Similar results have been obtained by Cloutier et al. (2007) in *Carapa guianensis*. The strongest effect of demographic thinning on SGS probably occurs at the seedling stage, not examined in our study, and where mortality is known to be high (Harcombe 1987). The comparison of SGS in sapling and adult stages in *D. guianensis* may thus have missed much of this thinning effect. Conversely, a higher inbreeding coefficient F_{IS} in saplings (0.12) than adults (0.05) suggests that demographic thinning through elimination of inbred trees was not completed for the sapling stage. This has already been observed in *D. guianensis* (Latouche-Hallé et al. 2003) and other tropical species (Lowman and Rinker 2004). An alternative hypothesis for deviation from the expected SGS patterns among cohorts (similar SGS in saplings vs. adults in *D. guianensis* in Nouragues) could be different histories of establishment of those cohorts in response to different abiotic conditions. This has been observed in *Jacaranda copaia*, another heliophilic species during its young stage, where a strong El Niño Southern Oscillation caused a large increase in fruit and seed production affecting the spatial genetic structure of the offspring cohort (Jones and Hubbell 2006).

Implications for conservation

Dicorynia guianensis populations in French Guiana have high genetic diversity, a continuous range with low to moderate genetic differentiation, low inbreeding, and weak to moderate spatial genetic structure, similar to other tropical tree species in the region with similar ecological characteristics (Vekemans and Hardy 2004; Degen et al. 2004; Hardy et al. 2006; Cloutier et al. 2007). Our data correspond to the first genetic assessment with nuclear markers at the regional level and within multiple stands that can serve as a reference for future genetic monitoring. The effects of logging, change of land use, and climate on the genetic diversity and structure of *D. guianensis* are difficult to detect at present because the onset of logging and strong human demographic growth are recent, corresponding to the last 0-2 generations for *D. guianensis* in French Guiana. A robust assessment of the impact of logging on *D. guianensis* populations should ideally be based on the analysis of juvenile individuals across generations (Lacerda et al. 2008) and larger number of genetic markers.

Timber extraction in the State owned permanent forest domain (DFP, 2.4 Mha) in French Guiana follows low-impact silvicultural rules (Guitet et al. 2014) with PEFC certification since 2012 and an extraction of a maximum of 5 trees/ha with a 65 years rotation (PEFC France 2016). Three different management zones have been defined for *D. guianensis* in the DFP based on similar climatic and geological criteria: East, Centre, and West. For *D. guianensis*, current silvicultural guidelines established based on forest inventories and studies of population dynamics recommend a minimum extraction diameter of 55 cm in the three largest zones: East, Centre, and West of the DFP, with a potential increase of the minimum extraction diameter to 65 cm in the East, where trees are larger and density is highest. They also recommend sparing isolated trees from exploitation and leaving one or two seed trees per aggregate, preferentially at their margin, to maximize seed rain and preserve genetic diversity within stands (Guitet et al. 2014). Our findings support the pertinence of considering separate management guidelines for the three DFP zones, specifically because of the genetic distinctiveness of the West. The data sets used did not allow us to robustly distinguish genetic structure among sampling sites in the Center and East, probably due to very low sampling size in some sites and the limited number of SSRs used. Current forest management in French Guiana has a favorable approach, taking into account multiple zones to represent environmental variability. In addition, and to cope with the current issues of climate change (Guyaclimat 2022) and strong human demographic growth (INSEE 2019), it is essential to preserve *D. guianensis* intraspecific genetic variation within these areas. The setting up of reference gene conservation sites that exclude selective logging and hunting within each DFP zone can be considered as an improvement of the current management. These sites should represent large populations with high genetic diversity and potentially with differential adaptations, to maximize overall high fitness and adaptive potential.

Genetic indicators based on genetic effective population size (N_e) and on population differentiation have been proposed for the monitoring of conservation status in all species (Hoban et al. 2020, 2022). In continuously distributed species with large populations such as forest trees where N_e is not easy to estimate (Fady and Bozzano 2021; Santos-del-Blanco et al. 2022), SGS provides valuable information for the conservation of genetic diversity: in *D. guianensis* genetic neighborhoods harbor dozens to hundreds of individuals in a few hectares indicating relatively large local breeding populations, e.g. $NS=116$ in a circle of radius 2σ corresponding to 30,6 ha in Regina. The relationship between NS and N_e is complex, but with $NS>4\pi$ ($=12.6$), the neighborhood size has no noticeable effect on the global effective population size (Nunney 2016), which is probably much larger in *D. guianensis*. We found that NS was lowest in Paracou with $NS=35$, an order of magnitude lower than in Eperon with $NS=313$. This lower NS in Paracou could potentially be due to hunting (see above), recent logging or simply be explained by natural metapopulation dynamics. It could further mean Paracou is at a higher risk of inbreeding and genetic erosion, although both H_e and F_{IS} do not indicate such problems, illustrating the different properties of these statistics. The obtained NS estimates can be used as genetic indicator values for reference (Major et al. 2021) in future studies to help disentangle the effects of metapopulation dynamics and selective logging on SGS. While the impact of logging in terms of numbers of individuals extracted remains moderate with a maximum of 5 trees extracted per ha (Guitet 2005), there may be an effect of dysgenic selection by extracting superior individuals (i.e., those who are largest and survive to adulthood) (Murawski et al. 1994; Lee et al. 2002).

Conclusion

We showed that *Dicorynia guianensis* shows a complex population genetic structure, probably the result of past demographic events combined with the effects of dispersal mechanisms at the local level and current abiotic factors such as the rainfall gradient at the regional level in French Guiana. Pleistocene drought periods may have had an impact on population size, genetic diversity, and its distribution in this drought sensitive species, and thus possibly its populations' capacity to adapt. It is now critical to gain insights into the adaptive potential of this ecologically and economically important species in the face of global climate change (Fargeon et al. 2016), especially considering the recent and ongoing rapid temperature increase, more pronounced dry seasons and predictions of up to 30% reduction in rainfall in French Guiana by 2100 (Guyaclimat 2022). In future studies, it will be particularly pertinent to examine genomic signatures of adaptive divergence at the regional scale, in the face of contrasting water regimes, in order to design management guidelines for improved conservation and sustainable use of this heavily exploited species.

Statements and Declarations

Author contributions

Conceptualization: M.H., N.T.; Methodology: N.T., V.T., M.H.; Formal analysis and investigation: J.B.; Writing - original draft preparation: J.B.; Writing - review and editing: J.B., N.T., V.T., I.S., S.B., O.B., S.G., S.T., M.H.; Funding acquisition: S.G., O.B., M.H., N.T.; Resources: V.T., I.S., S.B., O.B., S.G., S.T., M.H.; Supervision: M.H. The authors read and approved the final manuscript.

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Conflict of interest

The authors declare no competing interest.

Ethical declaration

The authors confirm that they follow the good scientific practice and all ethical standards requested by the journal. The authors have obtained access to genetic resources on the French national territory (APA standards, file number: 8360908).

Data Archiving Statement

This paper includes three datasets of five nuclear SSR markers of *Dicorynia guianensis* trees sampled in French Guiana: DS1 with n=647 trees sampled across 23 locations, DS2 with n=117 individuals from Paracou (published in Latouche-Hallé et al. 2003) and DS3 with n=502 trees from Regina and n=300 trees from Nouragues Grand Plateau. The data is supplied as raw data in a supplementary file for review purposes and will be deposited in the TreeGenes database (<https://treegenesdb.org/tpps>).

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