

Short-distance seed and pollen dispersal in both hunted and intact forests in the lower canopy African rainforest tree, *Coula edulis* Baill (Coulaceae)

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Abstract

Background

Mammal-dispersed tropical trees can face regeneration problems due to increasing hunting pressure. We studied the case of *Coula edulis* Baill (Coulaceae), an African rainforest tree that produces the 'African walnut', an essential food and income resource for rural communities in Cameroon. We compared gene flow and regeneration dynamics in three populations with contrasting levels of human disturbance and mammal abundance. Using 21 nuclear microsatellite markers, we estimated the outcrossing rate and contemporary seed and pollen dispersal distances, and we analyzed the fine-scale spatial genetic structure (FSGS) to infer historical gene dispersal distances.

Results

Juveniles were outcrossed while 22–30% of the seeds were selfed, suggesting the elimination of inbred seeds. The mean dispersal distances were relatively short for seeds (105–219 m) and pollen (173–358 m), both shorter in the most intact forest. Immigration rates were three to four times higher for pollen (33–71%) than for seeds (7–28%), indicating some long-distance pollen dispersal. FSGS was strong in all populations ($Sp = 0.023–0.036$), suggesting short-range historical gene dispersal distances consistent with contemporary estimates. We detected assortative mating, possibly due to higher flowering synchronicity between related individuals. The most disturbed plots had an inverted J-shaped trunk diameter structure, typical of continuous regeneration, while the intact forest had a complex diameter structure with a weak regeneration pulse.

Conclusions

Our results suggest that forest disturbance and mammal hunting do not significantly affect the dispersal distances of seed and pollen for *Coula edulis*, contrary to other mammals-dispersed trees. We hypothesize that the main dispersers are scatter hoarding rodents that are less impacted, or even facilitated, by hunting pressure. The species appears to regenerate better in disturbed forests, possibly due to a reduction in seed and seedling predators. However, natural populations are threatened by ongoing forest conversion into agriculture.

1. Background

Seed and pollen dispersal play a key role in the ecological and evolutionary dynamics of tree populations and communities [1–6]. It affects reproductive success, a fundamental trait for long-term population viability, and a key feature for species conservation [7]. It is also a determinant of the level of genetic variation within and between populations. It can also neutralize the potentially deleterious effects of genetic drift and be a source of new alleles within populations [8]. However, dispersal is a highly stochastic process, determined by the abundance and behavior of seed and pollen dispersal vectors, which can vary between years and populations [9, 10].

In tropical forest ecosystems, wildlife plays a key role in both pollination and seed dispersal [11]. Hence, gene flow in trees depends on this fauna, which is affected by hunting, habitat destruction, and forest fragmentation. Disruption of plant interactions with dispersers or pollinators can affect genetic variation within species [5, 12, 13], resulting in more structured and less cohesive gene pools, and increased isolation-by-distance over larger areas [14–17]. Although the consequences of human pressures on the gene flow dynamics of tropical forest trees vary across

species and contexts [18, 19], they have received a lot of attention in recent years [14–16, 20–25], but they are still very little documented in African forest trees [5, 26–31].

Characterizing gene flow requires molecular markers [32–36] such as microsatellites, which have been developed in recent years for several African tree species *Cylicodiscus gabunensis* [37], *Terminalia superba* [38], *Coula edulis* [39], *Pericopsis elata* [40], *Entandrophragma candollei* [41], and *Baillonella toxisperma* [42]. Gene flow can be characterized by direct approaches identifying parent-offspring pairs through parentage analyses [43], which estimate contemporary gene flow. However, this requires exhaustive sampling of the parental population in the study area [32, 44]. Alternatively, gene flow can be evaluated by indirect approaches, for example from the amplitude of fine-scale spatial genetic structure (FSGS) expected under limited seed and/or pollen dispersal in space, providing estimates of historical gene dispersal distance without distinguishing the respective roles of seed and pollen dispersal [33, 34, 45, 46]. However, to date, gene flow analysis of African rainforest trees has been carried out mainly in canopy dominant and light-demanding species [5, 26, 27, 30, 47] while many tree species are shade tolerant and remain below the canopy, characteristics that can affect seed and pollen dispersal efficiency.

In this work, the objective is to characterize gene flow and the FSGS of *Coula edulis* Baill (Coulaceae) in Cameroon, comparing three populations under contrasting anthropogenic pressures. *Coula edulis* is a hermaphroditic lower canopy tree endemic to the tropical rainforests of Africa. In Cameroon, its natural range is restricted to Atlantic forests [48], although some populations are found in semi-deciduous forests [49]. Its fruits are an important source of food and income for rural populations. The species is most likely shade tolerant. Natural seed regeneration appears to be rare, as seedlings have rarely been observed in the forest despite abundant fruiting [50, 51]. This could be explained by low germination rates 10–20% [52, 53] and/or predation of seeds and freshly germinated seeds by large and small mammals [53, 54]. Therefore, it is essential to understand the extent of contemporaneous and historical gene flow in different environments. More specifically, the objectives of the present study will be: (1) compare genetic diversity and inbreeding parameters between cohorts, (2) characterize fine-scale spatial genetic structure (FSGS) to infer historical gene dispersal distances (σ_g), (3) characterize contemporary seed and pollen dispersal and subsequently assess the impact of disturbance, (4) test for the presence of inbreeding due to selfing and / or assortative mating between adult trees, (5) test whether male and female reproductive success of individual trees is related to trunk diameter, (6) compare and deduce the impact of human disturbances on the dynamics of regeneration between the different populations.

2. Methods

2.1. Species description

Coula edulis Baill, commonly known as 'African walnut', is an endemic tree species of the tropical rainforests of the Guineo-Congolian region, mostly found in evergreen forests with occasional occurrences in semideciduous forests, and ranging from West Africa (Sierra Leone) to western Central Africa (southwestern DRC) [49, 55]. It produces edible fruits consumed by rural populations, who sell the kernels on the roadside or in markets in large cities [56, 57]. The wood of *Coula edulis* is heavy and virtually rotproof, with an average density of 1.01 at 12% moisture content [58], and used to make charcoal and as construction material for huts [59]. Its bark is used in traditional medicine as a decoction for the treatment of several diseases [60–62]. It belongs to the Coulaceae family, a very small pantropical family formerly included in the Olacaceae family, with three monotypic genera distributed on different continents [63]. It is a medium-sized tree reaching 25 m in height from the lower forest level and the understory of mature forests [57]. The fruits are globular or ellipsoid, 3.5 to 5 cm long, yellowish green when ripe. The rounded stone is made of a hard brown endocarp and the seed is single and spherical, 1.5–2.5 cm in diameter. The species is

described as nonpioneer and tolerates shade. The minimum flowering diameter is 10.6 cm, the regular fruiting diameter is 23 cm, and the average annual diameter increase of the species is 0.22 cm/year [64]. In Cameroon, flowering generally occurs between the end of the dry season and the beginning of the short rainy season (February to April), while fruiting occurs during the peak rainy season from July to October [57]. In its natural environment, camera traps revealed that seeds are an important food source for many animal species such as bush pig (*Potamochoerus porcus*) and forest elephant (*Loxodonta cyclotis*), which act as predators, while emin's rat (*Cricetomys emini*) and African brush-tailed porcupine (*Atherurus africanus*) act both as predators and dispersers [54].

2.2. Study sites and sampling

The study was carried out at three sites in Cameroon (Fig. 1). (1) The Campo Ma'an National Park (CMNP) site was chosen because of the abundance of mammalian fauna in this protected area. On this site, we still find large mammals such as forest elephants (*Loxodonta cyclotis*), chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla gorilla*), and mandrills (*Mandrillus sphinx*) [65]. A 400 ha (2 x 2 km) plot (2.31856°N, 10.17641°E) was established in a continuous *terra firma* forest pocket. (2) The Mbalmayo Forest Reserve (MFR) and (3) Fifinda sites were chosen because they are located in areas of fragmented forest cover and are subject to strong anthropogenic activities with the following consequences: (i) a dramatic decrease in fauna, especially large mammal and monkey populations; (ii) an increase in the collection of non-timber forest products (NTFPs) such as *Coula edulis*, *Irvingia gabonensis*, *Ricinodendron heudelotii*, *Garcinia kola* [66]. At the MFR site, we established a 400 ha plot (3.43584°N, 11.44020°E) surrounded by the Nyong river on its western, southern and eastern sides (Fig. 1). At the Fifinda site, we established an 18 ha plot (300 x 600 m) (3.19646°N, 9.98077°E) where the species was present in several fragments of the population. The plot was surrounded by swamps to the northwest, the Loukoundjé River to the south, and a forest area to the east, part of which had been converted into an agricultural plantation.

In each plot of each site, all individuals (adults and juveniles) were sampled and seeds were collected. A piece of leaf or cambium was sampled on each individual and dried in silica gel. The diameter at breast height (DBH) was measured 130 cm above ground or above the buttresses, if any. The diameters of stems smaller than 130 cm in height were measured 10 cm above ground. In the rare case of multiple stems at the height of measurement, the largest was selected. The geographical coordinates of each individual have been recorded using a handheld GARMIN GPS 64s and 66sr. The individuals were classified as juveniles or adults according to diameter. Adult trees are defined as all individuals capable of sexual reproduction, which is above 10.6 cm in DBH, according to [64]. Juveniles are defined as all individuals with DBH < 10.6 cm and height < 130 cm. On the MFR 400 ha plot, inventories were conducted from February to April 2021, during which time we collected 160 juveniles, 220 adults, and 104 seeds corresponding to seven families. We also collected 21 individuals outside the plot, which will be added to those in the plot as part of the analysis of the FSGS and genetic diversity parameters. Similarly, in June 2021, we collected 72 juveniles and 53 adults in the 18-ha Fifinda plot, and 15 individuals were also collected outside the plot. Inside the CMNP 400 ha plot, the surveys took place from January to February 2022, collecting 154 juveniles and 646 adults.

2.3. DNA extraction and genotyping

DNA was extracted from 25 mg of leaf or 35 mg of cambium dried with silicagel, or 25 mg of seed cotyledon using the NucleoSpin 96 Plant Kit (Macherey-Nagel), according to the manufacturer's instructions. We genotyped 1465 samples consisting of 960 adult trees, 401 juveniles, and 104 seeds with 21 nuclear microsatellites markers, following the protocol developed by [39]. For each sample, 1.3 µL of the PCR product was added directly to 12 µL Hi-Di Formamide (Life Technologies, Carlsbad, California, USA) and 0.3 µL MapMarker® 400 labelled with DY-632 (Eurogentec, Seraing, Belgium) and genotyped on an ABI3730 sequencer (Applied Biosystems, Lennik, The

Netherlands). Genotypes were analyzed using Geneious version 7.1.9. Only samples for which at least seven out of 21 loci were successfully amplified were used for subsequent analyzes. The final number of samples used for subsequent analyzes was 1457 after eight individuals with missing data were removed (that is, 0.55% of the samples). Pairwise relationship coefficients [67] were calculated using SPAGeDi v.1–5 [68] to check for the presence of duplicated individuals or clones, as the species is known for producing suckers. If such duplicates were identified, these samples were removed leaving only one sample per genotype (the largest one).

Figure 1 Localization of the three *Coula edulis* populations in Cameroon (top left; the gray shaded area represents the potential rainforest area) and sampling scheme in each population. Top right: sampling scheme in Fifinda, with exhaustive sampling in a 18-ha plot delineated by a rectangle. Bottom left: sampling scheme in CMNP, with exhaustive sampling in a 400-ha plot. Bottom right: sampling scheme in MFR, with exhaustive sampling of a 400-ha plot

2.4. Characterization of genetic diversity and inbreeding

We used SPAGeDi v.1–5 [68] to estimate the following genetic parameters for each locus, cohort (adults, juveniles, and seeds), and population: (i) number of effective alleles (N_{AE}), (ii) allelic richness expressed as the expected number of alleles among k gene copies ($A_{R(k)}$), (iii) expected heterozygosity (H_E), (iv) observed heterozygosity (H_O), and (v) inbreeding coefficient (F_{IS}). We also used INEst 1.0 [69] to estimate the corrected inbreeding coefficient (F_{ISc}), i.e., considering null alleles, for each cohort and population. Analysis of variance in R [70] allowed us to test for significant differences in these parameters of genetic diversity between cohorts and populations. Under inbreeding depression, we expect an increase in observed heterozygosity (H_O) and a decrease in heterozygosity deficiency (F_{IS}) with age.

2.5. Characterization of historical gene dispersal through fine-scale spatial genetic structure (FSGS)

At the population level, fine-scale spatial genetic structure (FSGS) was assessed by the relationship between genetic relatedness and spatial distance (kinship-distance curve) in each population. To do this, we used the genotypes of individuals (adults and juveniles) to estimate the kinship coefficients (F_{ij}) between individuals using the estimator of J. Nason [71] implemented in SPAGeDi v.1–5 [68] because of its robust statistical properties [34]. These F_{ij} are then regressed on the logarithm of the distance between individuals (d_{ij}), resulting in a regression slope (b_{LD}) [72]. To obtain a graphical representation of the decrease in kinship with spatial distance, means of F_{ij} per spatial distance interval between individuals were also calculated for eight intervals (in meters): 0 to 10, 10 to 20, 20 to 40, 40 to 80, 80 to 160, 160 to 320, and 320 to 640 and 640 to 1000. FSGS was assessed in each population, but also at the cohort level, and then tested by randomly swapping the positions of individuals (10000 randomizations). The statistic $Sp = -b_{LD}/(1 - F_1)$, which characterizes the strength of FSGS, was obtained for each population and cohort from the observed regression slope (b_{LD}) of F_{ij} over the logarithmic distance d_{ij} and the mean kinship coefficient measured in the first distance class (F_1) [34].

Assuming drift-dispersal equilibrium, we estimated the historical backward gene dispersal distance (σ_g) for each population using the method described in [46], based on the kinship-distance curve. We estimated the size of the Wright neighborhood, defined as $Nb = 4\pi D_E \sigma_g^2$ where D_E represents the effective population density and σ_g^2 is half the mean squared distance between parents and offspring, using the relationship $Nb = (F_1 - 1)/b_{LD}$ where the regression slope b_{LD} is calculated in a restricted distance interval $\sigma_g > d_{ij} > 20 \sigma_g$. The dispersal distance of the genes was estimated using SPAGeDi v.1–5 [68] assuming a range of effective population density (D_E). To this end, D_E was

estimated knowing that the mean population densities (D) of trees that flower and fruit regularly in *C. edulis* have a $DBH \geq 23$ cm [64]. These densities (D) were obtained from the inventory data of individuals in the three populations. We have $D = 1.39, 1.01$ and 1.22 ind ha^{-1} in the CMNP, MFR and Fifinda, respectively. Assuming that the ratio of effective population sizes to census sizes (N_e / N) generally ranges from 0.1 to 0.5 in plant populations [73], we used three estimates of effective population densities (D_E): $D_E = D/2, D/4$, and $D/10$. These values corresponded to $D_E = 0.7, 0.35$ and 0.14 ind ha^{-1} for CMNP, $D_E = 0.51, 0.25$ and 0.10 ind ha^{-1} for MFR, and $D_E = 0.61, 0.31$ and 0.12 ind ha^{-1} for Fifinda.

2.6. Characterization of seed and pollen dispersal through parentage analysis and the neighbourhood model

The neighborhood model implemented in NM π software using the maximum likelihood approach [35, 74] allowed us to model seed and pollen dispersal kernels, estimate the selfing rate, and infer the impact of DBH on reproductive success. The model was fitted using the spatial locations of the samples, their genotypes, and the reduced and centered DBH values of the adult trees. First, an analysis was performed for each population with juveniles and parents (individuals with $DBH \geq 10.6$ cm), which contributed to the identification of the most probable mothers and fathers of juveniles with a genealogical probability ≥ 0.8 . This confirmed some observations made in the field, where we found fruit remains under some individuals with a $DBH < 12$ cm.

An additional NM π analysis was performed between all mature trees in the MFR plot and seeds ($n = 104$). This allowed us to confirm or reject the identity of the most probable mother with a genealogy probability ≥ 0.8 . For seeds for which no mother was identified among available adults, we estimated the kinship coefficients (F_{ij}) between them using SPAGeDi v.1–5 and, by reordering the resulting kinship matrix, we were able to group these seeds into families and manually reconstruct a likely maternal genotype. A third NM π analysis was then performed for the MFR population, including four reconstructed maternal genotypes as potential adults.

NM π analyses between adults and juveniles characterized parameters such as: seed and pollen immigration rates (ms/mp), self-pollination rate (s), seed and pollen mean dispersal distance (ds/dp). The immigration rate was estimated by assessing the contribution of parents outside the sampling area (proportion of pollen/seeds originating from unsampled adults). The dispersal distance parameters are those of the fitted dispersal kernels, which describe the probability that an emitted seed or pollen will disperse from a starting position to a final position. The modelled kernels assumed a bidimensional power-exponential distribution coupled with von Misses distribution to account for anisotropy and are characterized by four parameters: the mean dispersal distance (ds or dp), the shape parameter (bs or bp , equals to 2 for a gaussian, 1 for an exponential, or < 1 for a fat-tailed distribution), a degree of anisotropy (ks or kp , equal to zero under isotropic distribution), and a direction of prevailing dispersal (as or ap) [33, 74, 75]. To determine whether the estimated seed and pollen dispersal kernel and the degree of sampling completeness could predict pollen and seed immigration rates, we used an R script described in [5] to simulate the contribution of unsampled trees to reproduction. For this aspect, we only used the CMNP population because it was in a continuous forest where *C. edulis* was well distributed outside the sampling plot.

For parents of offspring detected with a genealogical probability ≥ 0.8 , the distribution of their diameter was compared with that of all adult individuals in the plot. This allowed us to see which of the tree diameter classes contributed the most to pollination or established juveniles. Seed and pollen dispersal kernels were illustrated by showing the position of juveniles with respect to their mother (seed dispersal events) or of mother with respect to the father (pollen dispersal events) on two-dimensional maps.

2.7. Comparison of historical and contemporary gene flow estimates

To compare contemporary and historical gene dispersal estimates, we need to convert the respective estimates obtained by direct and indirect methods, because contemporary estimates through NM π describe pollen and seed dispersal under a power-exponential kernel (parameters dp , ds , bp , and bs), while historical estimates are expressed in terms of the mean squared parent-offspring distance (σ_g^2). To convert the d and b parameters into σ , we used the function (1) derived from [33].

$$\sigma^2 = 0.5 d^2 \Gamma(2/b) \Gamma(4/b) \Gamma(3/b)^{-2} \text{ (Eq. 1)}$$

where σ^2 is half of the mean squared parent-offspring distance; $d = dp$ or ds : mean pollen or seed dispersal distance; $b = bp$ or bs : shape of the pollen or seed dispersal kernel; Γ : gamma function.

This allowed us to obtain σ_p^2 and σ_s^2 , which represent the extent of pollen and seed dispersal distances, respectively. Eq. (2) then allowed one to estimate the contemporary distance of gene flow (σ_g) that can be compared with the corresponding estimates obtained by the historical method.

$$\sigma_g^2 = \sigma_s^2 + 0.5 \sigma_p^2 \text{ (Eq. 2)}$$

2.8. Biparental inbreeding and assortative mating

When gene flow is limited, biparental inbreeding (mating between relatives) can occur [76, 77], and can be further enhanced by assortative mating (preferential mating between relatives), for example, when flowering phenology is heritable. To test this, using the methodology highlighted by [44], we considered the mating pairs ($n = 115$) previously identified and compared for each unique pair ($n = 83$) their kinship coefficient (F_{ij}) with the one expected based on their spatial distance and the kinship distance curve (i.e., the mean F_{ij} between adults in the same distance interval), using a Student's t test. If the mean F_{ij} between pairs is significantly higher than expected, assortative mating would be inferred, while if it is significantly lower than expected by chance, inbreeding depression resulting from biparental.

2.9. Regeneration dynamics

We assessed the diametric distribution of individuals within each population to infer the dynamics of regeneration. Effective regeneration is evidenced when the number of young individuals is high enough to ensure the renewal of the species, typically leading to a decreasing number of stems with increasing diameter ("inverted J" distribution) [78, 79]. A deficit of regeneration appears when there are fewer individuals in the small-diameter classes, leading to a "bell" distribution [80, 81]. At the level of each population, we also inspected the distribution of cumulative numbers of juveniles according to their diameter to determine which of the diameter classes was the most represented.

3. Results

3.1. Characterization of genetic diversity, inbreeding and selfing rate

From each population, the parameters of genetic diversity did not differ significantly between the adult and juvenile cohorts. However, seeds collected in the MFR population showed significantly lower H_O and higher F_{IS} than juveniles and adults (Table 1). The coefficient of inbreeding, uncorrected for null alleles (F_{IS}), was significantly greater than

zero in all populations and cohorts, except for juveniles in Fifinda ($F_{IS} = 0.076$). This can be attributed to a low sample size (72 individuals). The estimates of inbreeding that account for the presence of null alleles (F_{ISc}) were close to zero, except for seeds in MFR, with $F_{ISc} = 0.145$ (Table 1).

The inbreeding coefficients were consistent with estimates of selfing rate based on identity disequilibrium, which were close to zero in adults and juveniles, but higher in seeds ($S = 0.13$). Direct estimates (NM π) confirmed the low selfing rate in juveniles (0 ± 0.004 in CMNP, 0.02 ± 0.01 in MFR, 0 ± 0.01 in Fifinda) and the much higher rate in seeds (0.30 ± 0.05 in MFR). More specifically, of the 104 seeds collected under seven trees in the MFR population, 17 (26%) selfed seeds were present under four trees. About 25% of the seeds collected could not be assigned to any of the seven trees under which they were collected, nor to any other adult tree, but after identifying four families within the latter and adding four reconstructed genotypes of the mothers of these families, a total of 31 seeds (30%) appeared self-fertilized. This indicates the expression of inbreeding depression between the seed and seedling stages in *C. edulis*.

Table 1
Parameters of genetic diversity and consanguinity of the different cohorts of the *Coula edulis* populations

Population	Cohort	<i>N</i>	<i>N_{AE}</i>	<i>A_R</i>	<i>He</i>	<i>Ho</i>	<i>F_{IS}</i>	<i>F_{ISc}</i>	<i>S</i> (SE)	<i>Sp</i> (SE)
CMNP	Juveniles	154	3.89	10.07	0.695	0.594a	0.146a*	0.037 (0.013–0.061)	0.039 (0.021)	0.021 (0.003)
	Adults	646	3.81	10.16	0.692	0.608a	0.122a*	0.018 (0.008–0.029)	0.022 (0.01)	0.024 (0.003)
MFR	Seeds	104	2.88	6.57	0.595	0.406a	0.319a*	0.143 (0.087–0.206)	0.13 (0.06)	-
	Juveniles	171	3.22	6.93	0.633	0.525b	0.171b*	0.031 (0.004–0.061)	0.08 (0.03)	0.047 (0.012)
	Adults	237	3.07	6.81	0.623	0.548bc	0.120bc*	0.011 (0.001–0.024)	0.02 (0.03)	0.032 (0.003)
Fifinda	Juveniles	72	3.46	7.59	0.651	0.602a	0.076a	0.040 (0.009–0.059)	0 (0.01)	0.033 (0.005)
	Adults	73	3.62	8.46	0.666	0.597a	0.104a*	0.028 (0.001–0.055)	0 (0.01)	0.024 (0.003)

N: sample size; *N_{AE}*: effective number of alleles; *A_R*: allelic richness ($k = 130$); *He*: expected heterozygosity (gene diversity corrected for sample size); *Ho*: observed heterozygosity; *F_{IS}*: inbreeding coefficient potentially biased by null alleles; *F_{ISc}*: inbreeding coefficient accounting for null alleles (95% posterior range); *S*: selfing rate based on identity disequilibrium; *Sp*: degree of fine-scale spatial genetic structure (FSGS); *SE*: standard error.

Letters for *Ho* and *F_{IS}*: within populations, values that share a common letter do not differ significantly ($P > 0.05$) in the analysis of variance. * Indicates $F_{IS} > 0$ at $P < 0.01$.

3.2. Characterization of historical gene flow through the fine-scale spatial genetic structure (FSGS)

In each population, the kinship coefficients (F_{ij}) decreased fairly linearly with the logarithm of geographic distance, as predicted in the context of isolation by distance (Fig. 2). The mean F_{ij} for the first distance class (< 10 m) ranged from 0.08 to 0.13 and decreased rapidly with distance, giving levels of FSGS in different populations ranging from $Sp = 0.036 \pm 0.004$ in MFR and 0.028 ± 0.003 in Fifinda to 0.023 ± 0.003 in CMNP. Similar high Sp values were obtained for juveniles and adults (Table 1).

Figure 2 Comparison of fine-scale spatial genetic structures (FSGS) of *C. edulis* trees in the three study sites, as assessed by the kinship coefficient (F_{ij}) plotted against geographical distances (in meters, on a logarithmic scale)

The indirect approach to estimate the gene dispersal parameters from the FSGS converged in each population under the highest assumed effective density, leading to neighbourhood sizes ranging from $Nb = 21$ (MFR) and 30 (Fifinda) to 83 (CMNP), and the extent of gene dispersal ranging from $\sigma_g = 182 \pm 15$ m (MFR) and 198 ± 18 m (Fifinda) to 307 ± 113 m (CMNP; Table 2). When the assumed effective densities were lower, the method did not always converge but led to higher σ_g estimates in the MFR (268 ± 30 m or 506 ± 66 m; Table 2).

Table 2
Parameters for the estimation of historical backward gene dispersal of different populations of *Coula edulis*.

Population	D (ind ha ⁻¹)	D_E (ind ha ⁻¹)	Nb	σ_g (m)
CMNP		0.70	83 ± 70	307 ± 113
	1.39	0.35	NA	NA
		0.14	NA	NA
MFR		0.51	21 ± 4	182 ± 15
	1.01	0.25	23 ± 5	268 ± 30
		0.10	32 ± 8	506 ± 66
Fifinda		0.61	30 ± 5	198 ± 18
	1.22	0.31	28 ± 19	269 ± 91
		0.12	NA	NA

D : density of trees that flower and fruit regularly (DBH ≥ 23 cm); D_E : assumed effective population density (1/2, 1/4 or 1/10 of D); Nb : Wright's neighbourhood size $\pm$ SE; σ_g : gene dispersal distance $\pm$ SE; NA: indicates that the estimation procedure did not converge.

3.3. Characterization of gene flow through direct analyzes

Taking into account only the progeny for which the mother and/or father were identified with probability $P \geq 0.8$ following NM π analyses, we found that mothers and fathers were assigned, respectively, to 105 and 44 of the 154 juveniles in CMNP, 103 and 62 of the 171 juveniles in MFR, 32 and 14 of the 72 juveniles in Fifinda. For the 104 seeds sampled in MFR, 76 were mothered by seven trees under which they were harvested, while 66 were fathered by 13 sampled trees. When NM π analysis was run again after adding four reconstructed maternal genotypes based on the

genotypes of seeds not assigned to any adult tree, we found that 96 seeds were mothered by 11 trees and 73 seeds were fathered by 17 trees.

The seed immigration rates based on NM π analyses of juveniles ranged from $ms = 0.07 \pm 0.03$ in MFR and 0.15 ± 0.03 in CMNP to 0.28 ± 0.07 in Fifinda (Table 3). Pollen immigration rates were higher but followed the same trend among populations, ranging from $mp = 0.33 \pm 0.05$ in MFR and 0.59 ± 0.05 in CMNP to 0.71 ± 0.08 in Fifinda (Table 3). For seeds sampled in MFR, $ms = 0.20 \pm 0.01$ and $mp = 0.17 \pm 0.04$ when the reconstructed maternal genotypes were integrated.

The mean seed dispersal distances based on the estimated kernels were rather short, ranging from $ds = 105$ m in CMNP and 131 m in MFR to 219 m in Fifinda, but with overlapping confidence intervals (Table 3). Therefore, seed dispersal was certainly not higher in the forest with the most intact fauna. These kernels were moderately leptokurtic (bs ranging from 0.5 to 0.8 , Table 3) and anisotropic, at least in MFR and CMNP (ks ranging from 0.3 to 0.9), with more dispersal events southward (as ranging from 0.41 to 0.57), a trend also visible when illustrating inferred seed dispersal events around the mother trees (Fig. 3). Of the 105 seed dispersal events detected in CMNP, 59 (56.2%) occurred within 100 m and only two were beyond 300 m (Fig. 3). Similarly, in MFR, of the 103 seed dispersal events detected, 62 (60.2%) occurred within 100 m and a few beyond 500 m (Fig. 3). In Fifinda, of the 32 seed dispersal events detected, 87.5% occurred within 100 m (Fig. 3) but the small sampling area did not allow detection of long-distance dispersal events.

The mean pollen dispersal distances based on the estimated kernels were greater than for seeds, ranging from $dp = 173$ m in CMNP and 211 m in MFR to 358 m in Fifinda (but note the broad confidence interval for Fifinda, encompassing the estimates of ds of the other populations; Table 3). These kernels were moderately leptokurtic to near Gaussian (bp ranging from 0.5 to 1.68 , Table 3) and anisotropic in MFR ($kp = 1.04 \pm 0.33$), with more dispersal events toward the northeast ($ap = 0.13$), a trend also visible in Fig. 3 (MFR) but not in the other populations. Of the 44 pollen dispersal events detected in CMNP, 14 (31.8%) occurred within 100 m and 14 (31.8%) beyond 200 m (Fig. 3). Of the 62 pollen dispersal events detected in MFR, 36 (58%) occurred within 100 m and two reached 600 to 700 m (Fig. 3). Of the 14 pollination dispersal events detected in Fifinda, 11 occurred within 100 m (Fig. 3).

Figure 3 Spatial representation of dispersal events around the source inferred by parentage analyses for pollen (+) and seeds (●) in different populations. Dispersal events inferred with a probability ≥ 0.8 are represented after centring the latitudinal and longitudinal displacements based on the source coordinates (0, 0). The circle centered on the source has a radius of 100 m.

Table 3

Seed and pollen dispersal parameters ($\pm$ standard error) of different populations of *C. edulis* estimated using the neighbourhood model implemented in NM π .

Parameter	CMNP	MFR (Juveniles)	MFR (Seeds)	Fifinda
Density of adults per ha (diameter $\geq$ 23 cm)	1.39	1.01	1.01	1.22
Selfing rate (<i>s</i>)	0 ± 0.004	0.02 ± 0.01	0.30 ± 0.05	0 ± 0.01
pollen immigration rate (<i>mp</i>)	0.59 ± 0.05	0.33 ± 0.05	0.17 ± 0.04	0.71 ± 0.08
Mean kernel pollen dispersal distance (<i>dp</i>)	173 m [141–223] ^a	211 m [151–348] ^a	65 m [48–97] ^a	358 m [156– ∞] ^a
Shape of pollen dispersal kernel (<i>bp</i>)	1.68 ± 0.48	0.79 ± 0.18	-	0.5 ± 0.1
Pollen dispersal anisotropy (<i>kp</i>)	0.31 ± 0.34	1.04 ± 0.33	-	
Pollen dispersal prevailing direction (<i>ap</i>)	0.86 ± 0.15	0.13 ± 0.05	-	
seed immigration rate (<i>ms</i>)	0.15 ± 0.03	0.07 ± 0.03	0.2 ± 0.01	0.28 ± 0.07
Mean kernel seed dispersal distance (<i>ds</i>)	105 m [86–140] ^a	131 m [99–197] ^a	-	219 m [134–599] ^a
Shape of seed dispersal kernel (<i>bs</i>)	0.8 ± 0.16	0.73 ± 0.14	-	0.5 ± 0.1
Seed dispersal anisotropy (<i>ks</i>)	0.30 ± 0.16	0.9 ± 0.19	-	
Seed dispersal prevailing direction (<i>as</i>)	0.41 ± 0.09	0.57 ± 0.03	-	
Effect of dbh on female fitness (<i>g</i>)	0.83 ± 0.10	0.41 ± 0.10	-	0.57 ± 0.15
Effect of dbh on male fitness (<i>b</i>)	0.59 ± 0.17	0.61 ± 0.15	-	0.39 ± 0.34

^a 95% confidence interval when both the shape and the mean distance of dispersal kernels are estimated.

- indicates parameters that were not estimated

Although pollen and seed dispersal distances were rather small ($dp = 173\text{--}358$ m; $ds = 105\text{--}219$ m, Table 3), we had a substantial proportion of immigrant pollen ($mp = 33\text{--}71\%$) and a small proportion of immigrant seeds ($ms = 7\text{--}28\%$) that must originate from trees outside our sampling areas or from adult trees missed during inventories.

When controlling whether dispersal kernels could explain the observed immigration rates in the CMNP population by simulating dispersal events from trees surrounding the 400 ha sampling area [5], our simulations predicted seed immigration rates (ms) between 10.5 and 12.5%, a range close to the estimated ms at 15%, suggesting that the seed dispersal kernel parameters are probably reliable. On the contrary, for pollen, our simulations predicted a pollen immigration rate (mp) between 16 and 17%, a range far below the estimated mp at 59%, leaving a gap of nearly 42% of pollen that is not described by the inferred kernel. When forcing the estimation of pollen dispersal curve parameters to be more leptokurtic ($bp = 0.25$) and adjusting $dp = 300$ m, the predicted immigration rate (mp) reached 25%, which remains far from the estimated value. Hence, a significant proportion of pollen disperses over long distances, and the 400 ha sampling area remains too small to detect these long-distance dispersal events.

3.4. Comparison of historical and contemporary estimates of gene flow

Following Equations (1) and (2), the estimated parameters of the pollen and seed dispersal kernel (dp , ds , bp and bs) result into $\sigma_s = 121, 95, 224$ m, $\sigma_p = 191, 140, 367$ m and $\sigma_g = 181, 137$ and 343 m for the populations of CMNP, MFR, and Fifinda, respectively. These contemporary σ_g estimates are consistent with historical σ_g estimates obtained in MFR (182–506) and Fifinda (198–269) but, in CMNP, they tend to be smaller than historical estimates (307; Table 2). As simulations showed that contemporary pollen dispersal distances were underestimated, at least in CMNP, observing higher indirect σ_g estimates is not unexpected. Thus, there is no evidence that contemporary gene dispersal distances differ from historical ones.

3.5. Biparental inbreeding and assortative mating

The mean value of the kinship coefficient (F_{ij}) observed between the 83 pairs of mates identified with probability $P \geq 0.8$ in the MFR population, after the exclusion of self-fertilization events, reached $F_{ij} = 0.092 \pm 0.013$, which is a significantly higher than the mean value of $F_{ij} = 0.064 \pm 0.003$ expected based solely on the spatial distances between mates (t test; $P = 0.034$). This indicates that mating between related individuals occurs more frequently than expected by chance, suggesting assortative mating. On the contrary, there is no evidence of biparental inbreeding depression, which would have led to a lower level of relatedness between mates of established juveniles than expected by chance.

3.6. Diametric structure and its impact on reproductive success

The effect of DBH on reproductive success was inferred through NM π analyses (Table 3) and by comparing, for each population, the diametric distribution of all trees, inferred mothers, and inferred fathers (Fig. 4). The diameter of the trunk positively affected the reproductive success of both the functions of female (g ranging from 0.41 in MFR and 0.57 in Fifinda to 0.83 in CMNP) and male (b ranging from 0.39 in Fifinda to 0.59 in CMNP and 0.61 in MFR). However, in Fifinda, where we identified the father of only 14 juveniles, the standard error on b (0.34) was as large as the estimate (0.39; Table 3).

Whatever the population, both maternity and paternity in *C. edulis* began at a relatively small diameter (smallest mother or father: 12.6 cm in CMNP, 12.0 cm in MFR, 11.1 cm in Fifinda). Large trees contributed disproportionately to regeneration, particularly in the most intact forests: trees with a DBH ≥ 50 cm mothered or fathered 67% of juveniles in CMNP, 31% in MFR, and 9% in Fifinda. The very low value observed in Fifinda is due to the low proportion of trees > 50 cm (3.5% in Fifinda, compared to 15% in MFR and 34% in CMNP). The median DBH of mothers and fathers were, respectively, 53.3 and 53.2 cm in CMNP, 39.5 and 40.1 cm in MFR, 24.7 and 27.6 cm in Fifinda.

Figure 4 Comparison of the DBH structures of all trees with that of inferred mothers and fathers of juveniles in different populations of *Coula edulis*

3.7. Diameter distribution analysis and regeneration

The diametric distribution of mature trees differed strikingly between populations (Fig. 4). In the CMNP population, *C. edulis* shows a multimodal distribution of DBH, with high numbers of individuals in the juvenile class but also in the 40–50 cm class, before observing decaying numbers with higher diameter classes (Fig. 4). On the contrary, in the MFR and Fifinda populations, the observed diametric distributions follow "inverted J" shapes, indicating a high number of individuals in the juvenile class ($n = 169$ and 74 in MFR and Fifinda, respectively) and a decrease in the number of individuals with higher diameter classes (Fig. 4).

Furthermore, among juveniles from MFR (stems with DBH < 10.6 cm), 75% had a diameter between 0 and 2 cm (Fig. 5), suggesting a recent regeneration burst, while in Fifinda and CMNP, the cumulative abundance of stems increased nearly linearly with DBH, indicating a rather uniform distribution within the 0–10 cm DBH class (Fig. 5). Therefore, the most disturbed and defaunated populations (Fifinda, and to a lesser extent MFR) showed a pattern indicative of good regeneration (“inverted J” distribution), while the most preserved forest (CMNP) showed a regeneration deficit. However, in Fifinda, no large trees were found (maximum DBH = 58.5 cm compared to 99.5 cm in MFR and 110 cm in CMNP), possibly due to logging by the villagers, as we observed a large number of mature trees that had been cut in the plot to harvest their fruits.

Figure 5 Cumulative relative frequency of juveniles (DBH < 10.6 cm) with diameter in different populations of *Coula edulis*

4. Discussion

This study characterized genetic diversity, mating system, historical and contemporary gene flow, and regeneration within three *C. edulis* populations showing similar densities of adult trees but contrasted levels of human disturbances. We now discuss the potential impacts of human disturbances on the dynamics of the *C. edulis* population.

4.1. Effects of disturbance on genetic diversity and inbreeding

Our results show similar levels of genetic diversity between populations and between cohorts (Table 1). As in most other tropical species, we found that *C. edulis* is a predominantly outcrossing species, although it has considerable potential for seed self-fertilization (22–30% in the MFR population). This rate is substantially higher than that observed at seed level in several other African tree species (e.g. 4% in *Cylicodiscus gabunensis* [26]). Our results indicate that self-pollinated seeds rarely produce offspring, as suggested by the decrease in inbreeding between the seed ($F_{ISc} = 0.143$) and juvenile ($F_{ISc} = 0.031$) cohorts (Table 1), but also by the very low rate of self-fertilization in juveniles (0 to 2%), inferred through NMπ analyses (Table 1). This high rate of self-fertilization at the seed level could result from limited pollen dispersal and the absence of efficient prezygotic mechanisms avoiding selfing (e.g. self-incompatibility system). We ignore if self-fertilized seeds fail to germinate and/or if the resulting seedlings die early, but the inbreeding depression this reflects implies a substantial reproductive cost.

Self-fertilization rates in *C. edulis* juveniles are close to the 3% obtained by [26] at the juvenile stage of *C. gabunensis* and consistent with less than 10% found in other tropical tree species [21]. Higher rates of self-fertilization in juveniles were reported in a few African species 20% in *E. suaveolens* [29]; 20–40% in *B. toxisperma* [30]; and 54% in *Pericopsis elata* [47], although adults were not inbred (except in *P. elata*). Therefore, inbreeding depression manifested essentially between the seed and juvenile stages in *C. edulis*, while it was generally detected between the juvenile and adult stages in other African species [29, 30, 47]. Inbreeding depression could explain a large number of regeneration failures during early life stages in tropical tree species that are predominantly outcrossing but have considerable self-fertilization potential [82].

In addition to selfing, biparental inbreeding results from limited seed and pollen dispersal but also some level of assortative mating, possibly due to more synchronous flowering between related than unrelated adults [83]. Assortative mating has also been observed in other African species such as *Erythrophleum suaveolens* [5, 84] and *Entandrophragma cylindricum* [44], and a genetic determinism of flowering phenology was shown in *Milicia excelsa* [85]. Biparental inbreeding does not seem to cause substantial inbreeding depression in *C. edulis*; otherwise, it would

have erased the signal of assortative mating. Given that inbreeding patterns did not differ between populations, there is no evidence of an impact of human disturbances on inbreeding in *C. edulis*.

4.2. Effects of disturbance on fine-scale spatial genetic structure (FSGS)

The presence of a FSGS is a common phenomenon in tree species, depending on their reproductive system, population density, seed dispersal vectors, and, to a lesser extent, pollen dispersal [34]. In this study, high levels of FSGS were detected in each population and could be characterized by a near-linear decay of relatedness with the logarithm of the distance (Fig. 2). This type of genetic structure results from limited gene dispersal and locally interacting demographic and environmental factors [21, 34, 86]. The strength of FSGS, measured by the Sp statistic, can be compared for some African tropical forest trees reviewed by [21], and [47] for African species and through recent meta-analyses [23, 87]. Values for *C. edulis* ($Sp = 0.023–0.036$) were characteristic of trees dispersed over short distances by wind, gravity, or rodents (mean $Sp = 0.023$ [21]), which can be explained by the combination of limited seed and pollen dispersal. *Coula edulis* seeds are dispersed by small mammals such as scatter-hoarding rodents, which are known to be short-distance dispersers [88, 89] and seed predators [90, 91].

When comparing different cohorts, high FSGS was found in both juveniles and adults within each population (Table 1). These results contrast with those of [92] and [93] who have shown that human-induced disturbance of habitat and seed dispersal behavior affected the FSGS. Work on *Diospyros crassiflora*, the ebony tree dispersed by forest elephants in Central Africa, showed that high FSGS is observed among juveniles in defaunated forests, despite low FSGS among adults, while very low FSGS is found both among juveniles and adults in intact forests [94]. However, for *C. edulis*, anthropogenic degradation of MFR and Fifinda habitats could alter the quality of microhabitats and the conditions for the establishment and survival of juveniles [95–97]. This should affect the strength of FSGS, as observed in other studies [98, 99], but such an effect is currently not visible in the different populations of *C. edulis* studied, all of which had high but similar Sp values. Thus, there is no evidence of human impact on the FSGS of *C. edulis*.

4.3. Effects of disturbance on contemporary gene flow

There was little variation in the estimated seed and pollen dispersal parameters between the different populations of *C. edulis*. Pollen dispersal distances were always considerably longer than seed dispersal distances. This is consistent with previous studies that have reported more extensive pollen than seed dispersal distances in most tree species [5, 26, 44, 47, 100]. Consistently, pollen immigration rates ($mp = 33–71\%$) are substantial, approaching values found in other African trees (e.g. 51% for *Distemonanthus benthamianus* within an area 6.56 km² [5], 71% for *Cylicodiscus gabonensis* within an area 839 ha [26]). The higher seed and pollen immigration rates (ms , mp) observed in Fifinda can be explained by the relatively small size of the exhaustively sampled plot (18 ha instead of 400 ha). Similarly, the lower ms and mp values at MFR than at CMNP can be explained by the position of the 400 ha MFR plot, next to a river and inundated forests inhospitable for *C. edulis*, so that *C. edulis* did not occur in the vicinity of the plots along two of its sides, while the 400 ha CMNP plot was surrounded by forests where *C. edulis* occurred at similar densities in all directions.

The fact that in the CMNP plot the pollen immigration rate predicted from the estimated pollen dispersal kernel (16–25%) was much lower than the measured immigration rate (59%) indicates that a substantial proportion of pollen disperse over longer distances than assumed by the dispersal kernel. Hence, the area of 400 ha delimited for estimating pollen dispersal remains too small to capture most dispersal events, a situation reported in other studies [5, 26]. Keeping this caveat in mind, we found that the estimated mean pollen dispersal distances ($dp = 173–358$ m)

in *C. edulis* are lower than those found for African canopy species: 2500 m in *C. gabunensis* [26], 942 m in *P. elata* [47], 506 m in *E. cylindricum* [44], 294 m in *E. suaveolens* [5]. Relatively low pollen dispersal distances in *C. edulis* suggest that it might be pollinated by relatively small insects, as shown for other sub-canopy trees [101], which might result in shorter pollen dispersal distances [102].

Although we inferred relatively low mean seed dispersal distances ($ds = 105\text{--}219$ m) in *C. edulis*, they are not so different from those of some large African forest canopy trees dispersed by wind ($ds = 184$ m for *C. gabunensis* [26], 71 m for *D. benthamianus* [5]) or animals 175 m for *E. suaveolens* [5]. Camera trap observations on MFR and CMNP plots (unpublished) showed that the main dispersers are small mammals such as the rodents *Cricetomys emini* (Emin's rat), *Atherurus africanus* (porcupine), and *Heliosciurus rufobrachium* (squirrel). This is also confirmed by [54] in the forests of Gabon. According to [90] and [91], rodents are known to be short-distance dispersers. Although the Fifinda and MFR populations are experiencing human disturbances, this has not had a significant impact on seed dispersal patterns, indicating that the dispersal mechanisms have not changed in recent years. Hunting is known to negatively affect large wildlife but small mammal populations tend to resist, and sometimes proliferate, in hunted forests [103, 104], while they are the main dispersers of *C. edulis* seeds [54]. The lack of long-distance seed dispersal in CMNP also suggests that forest elephants act only as predators of *C. edulis* seeds, which is supported by observational studies and monitoring of seed germination in elephant dung [54]. This situation contrasts with the case of ebony trees, *D. crassiflora*, where long-distance seed dispersal prevails in intact forests hosting forest elephants, while seed dispersal is much more limited in deforested areas [94].

4.4. Comparison of historical and contemporary estimates of gene flow

Our results indicate that a significant fraction of the pollen-mediated gene flow of the *C. edulis* population of the sampled plot comes from outside. This was underestimated in the NM π analyses, so it is not surprising that the direct method produced lower σ_g values than the indirect method. When this fraction of pollen-mediated gene flow is taken into account, the σ_g values estimated by direct and indirect methods converge. The similarity between the contemporary and historical distances of gene dispersal confirms that the large mammal defaunation resulting from hunting did not significantly affect gene dispersal in *C. edulis*. In fact, defaunation generally affects large mammals [103–105] which can lead to an increase in populations of small mammals [89, 106] because they are less negatively affected by defaunation [107]. Therefore, by relying on small mammals for their dispersal, *C. edulis* populations appear resilient to the hunting effect of human disturbances.

4.5. Determinants of tree reproductive success

Our results show that the trunk diameter (DBH) positively affects the reproductive success of *C. edulis* trees, for both male and female functions (Table 3), as reported in other tree species [5, 26, 44, 47]. Our results show that all classes of DBH (except trees with DBH < 10.6 cm) contribute to reproduction (Fig. 4), which means that both maternity and paternity start early in this species, as the minimum diameter of flowering and fruiting was 11.1 cm. This is in agreement with our observations in the field, where we found some fruit remains under the crown of trees with DBH < 12 cm. This is corroborated by the results obtained by [64] who found that the minimum flowering diameter was 10.6 cm. The fact that *C. edulis* flowers at this early stage can be explained by the fact that it is a slower growing species than emergent tree species that have larger flowering diameters [108–110].

4.6. Effects of disturbance on the natural regeneration of *Coula edulis*

The DBH structures differed between the *C. edulis* populations (Fig. 5): the inverted J structure of the MFR and Fifinda populations indicates good regeneration, whereas this is not the case for the CMNP. The “inverted J” distribution was also reported by [111] in a population of *C. edulis* from south-eastern Cameroon and by [112] in Gabon. A possible explanation for better regeneration in hunted forests is that *C. edulis* seed dispersers are resilient, or even promoted, by hunting activities [103, 104] while some of their seed predators are selectively hunted. An alternative explanation is that the opening of the forest due to human disturbances benefits the regeneration of *C. edulis*. Disturbances in the MFR and Fifinda populations may have altered the microhabitat conditions in favor of the establishment and survival of *C. edulis* juveniles compared to the CMNP population (Fig. 6). Since *C. edulis* is a shade-tolerant species, it was a priori expected that the opening of the forest by human disturbances would lead to higher mortality of juveniles exposed to light, whereas this is not the case here, where we observe a good regeneration as for light-demanding species. Similar results are reported in *D. crassiflora* by [94] who observed good regeneration in defaunated forests compared to intact forests, despite the much less efficient seed dispersal. On the other hand, our results differ from the conclusions of [113, 114] who showed low regeneration in *Leptonychia usambarensis* and *Virola flexuosa*, respectively, in fragmented forests with high deforestation. Our results also differ from those obtained in Afrotropical forests, where according to [89] hunting-induced defaunation drives increased seed predation and decreased seedling establishment of commercially important tree species. However, the low number of large-diameter individuals in the different populations can be explained by the fact that the main trunk dies at a certain age and produces shoots that later take over [115].

5. Conclusions

Our study shows that the dispersal distances of *Coula edulis* seed and pollen are limited and do not differ significantly according to the level of human perturbation and defaunation, and did not change over time. This shows that the adverse effects of defaunation cannot be generalized to all tree species. Our results also showed higher recruitment in the more disturbed forests, possibly due to better access of the understory to sunlight and / or lower predation of seeds and seedlings. This calls into question the sciaphilic nature of the species. In this study, we showed a high rate of self-fertilization and inbreeding in seeds, followed by a strong inbreeding depression between the seed and juvenile stages. This, combined with the high predation of seeds and freshly germinated seedlings, may explain the low number of seedlings observed in some populations despite the high fruiting of the species. Despite the apparent resilience of *C. edulis* in the face of hunting pressures, it is important to conserve the remaining populations of *C. edulis* to ensure that the current level of genetic diversity is maintained, both for the conservation and domestication of this commercially important species.

Abbreviations

CMNP: Campo Ma'an National Park; MFR: Mbalmayo Forest Reserve; SSR: Simple sequence repeat; DBH: Diameter at Breast Height; DRC: Democratic Republic of the Congo.

Declarations

Ethical approval

Samples from Cameroon (Mbalmayo, Fifinda) were collected with a research permit granted by MINRESI (000102/MINRESI/B00/C00/C10/C13).

Conflict of interest

The authors declare that they have no conflict of interest.

Consent for publication

Not applicable

Author Contribution

N.G.K., B.S. and O.J.H. conceived the research. N.G.K. collected the data. N.G.K. and S.S. performed the genotyping. N.G.K and O.J.H. conducted data analyses. N.G.K. wrote the first draft and all authors contributed to the final version of the manuscript.

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Data availability statement

The microsatellite datasets analyzed during the current study are available in the Zenodo repository, <https://zenodo.org/uploads/13889553>

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Figures

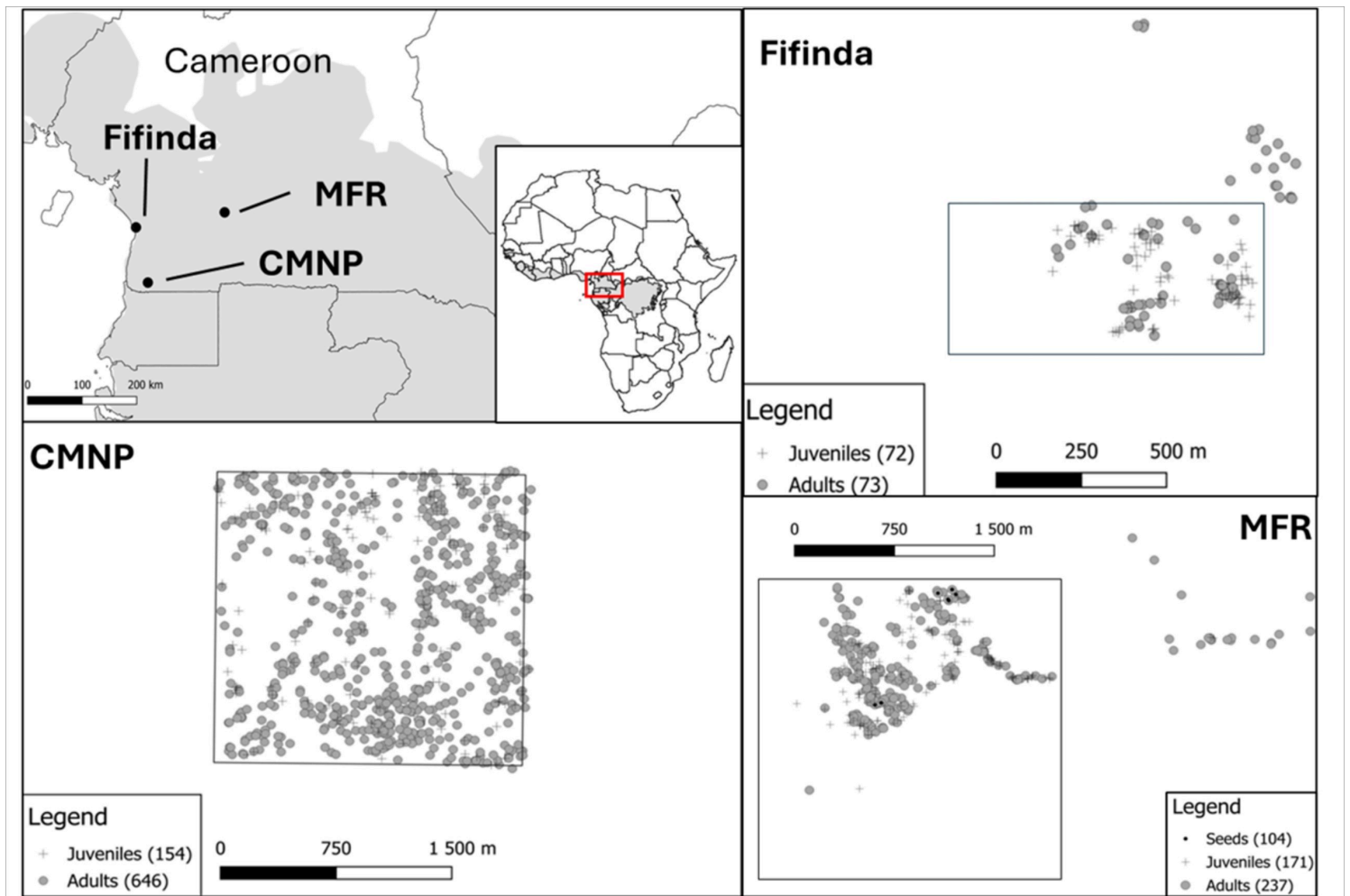


Figure 1

Localization of the three *Coula edulis* populations in Cameroon (top left; the gray shaded area represents the potential rainforest area) and sampling scheme in each population. Top right: sampling scheme in Fifinda, with exhaustive sampling in a 18-ha plot delineated by a rectangle. Bottom left: sampling scheme in CMNP, with exhaustive sampling in a 400-ha plot. Bottom right: sampling scheme in MFR, with exhaustive sampling of a 400-ha plot

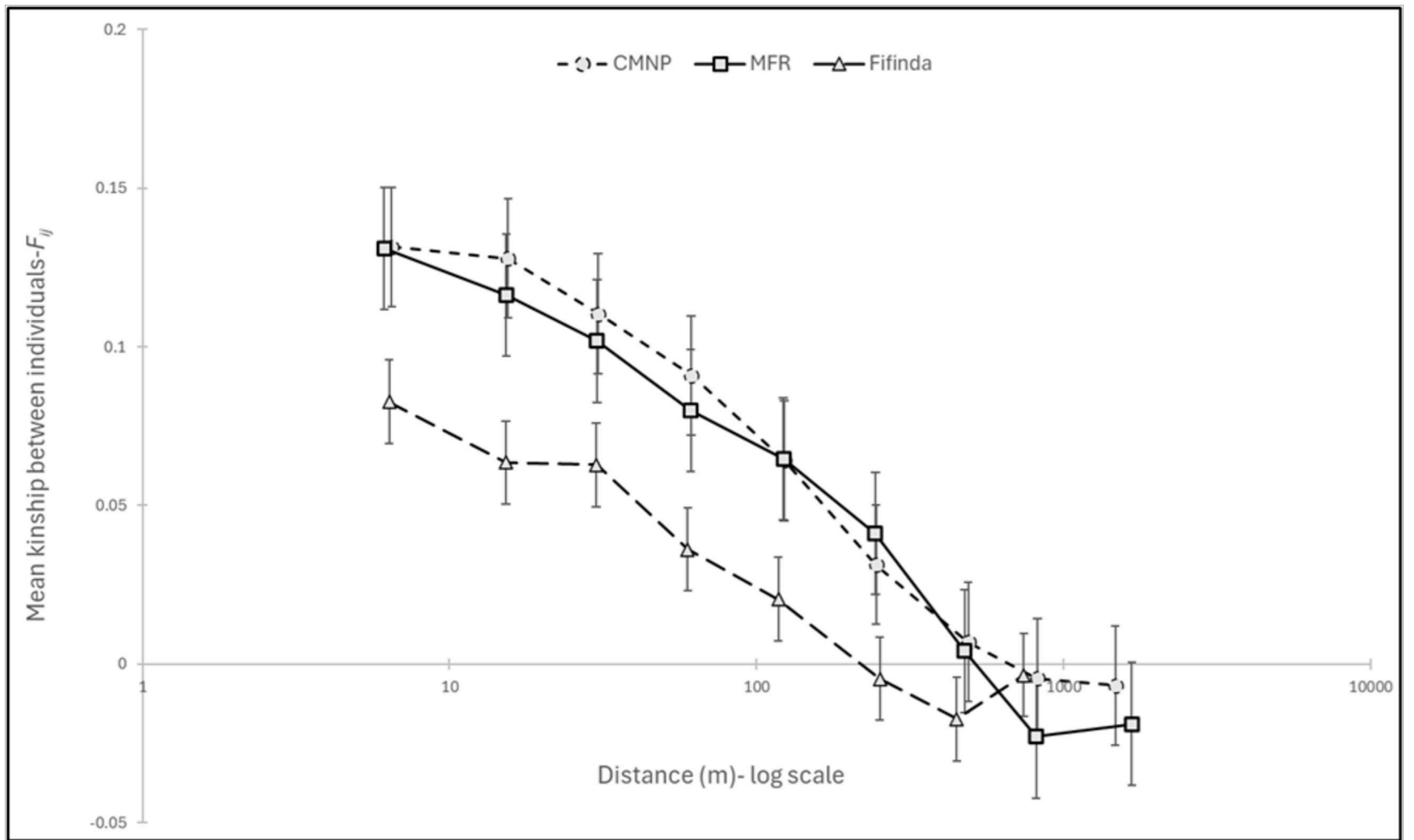


Figure 2

Comparison of fine-scale spatial genetic structures (FSGS) of *C. edulis* trees in the three study sites, as assessed by the kinship coefficient (F_{ij}) plotted against geographical distances (in meters, on a logarithmic scale)

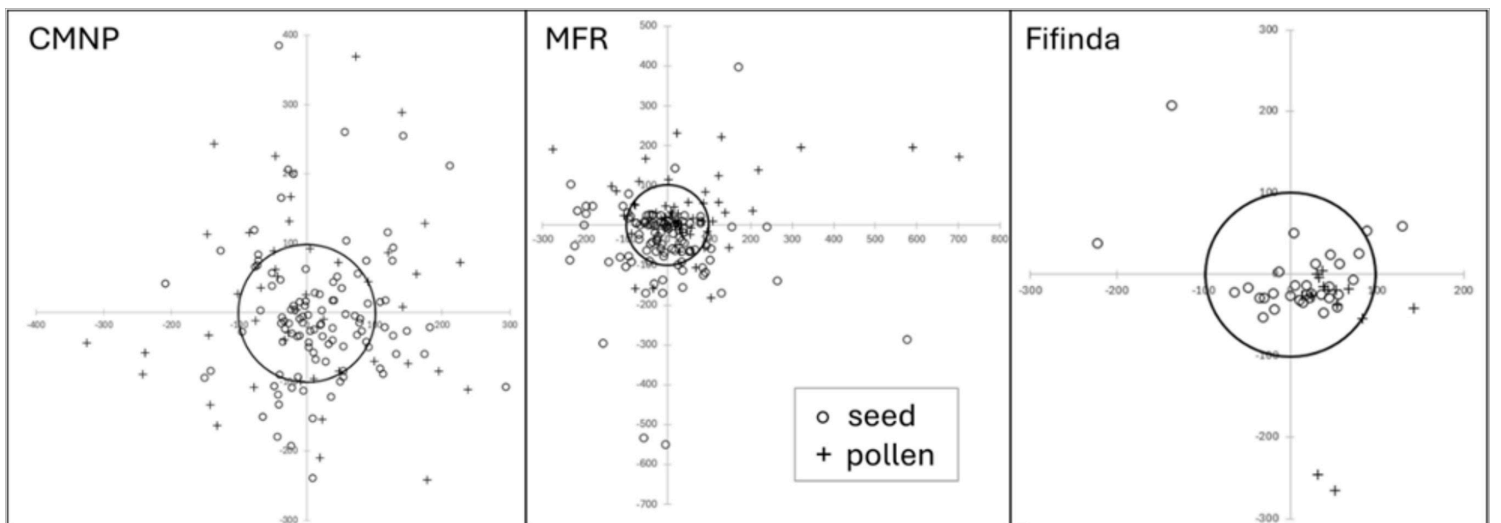


Figure 3

Spatial representation of dispersal events around the source inferred by parentage analyses for pollen (+) and seeds (●) in different populations. Dispersal events inferred with a probability ≥ 0.8 are represented after centring the latitudinal and longitudinal displacements based on the source coordinates (0, 0). The circle centered on the source has a radius of 100 m.

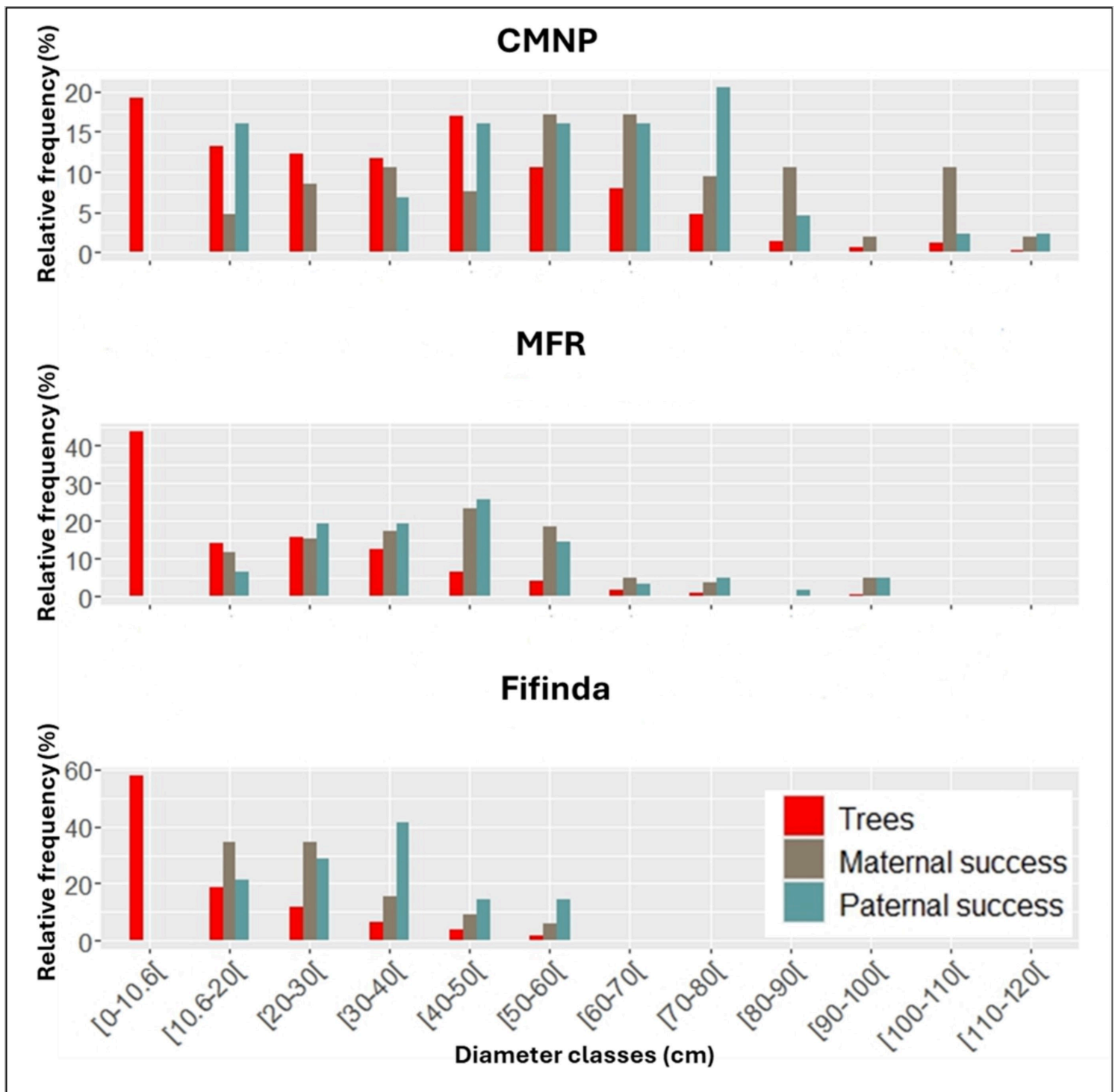


Figure 4

Comparison of the DBH structures of all trees with that of inferred mothers and fathers of juveniles in different populations of *Coula edulis*

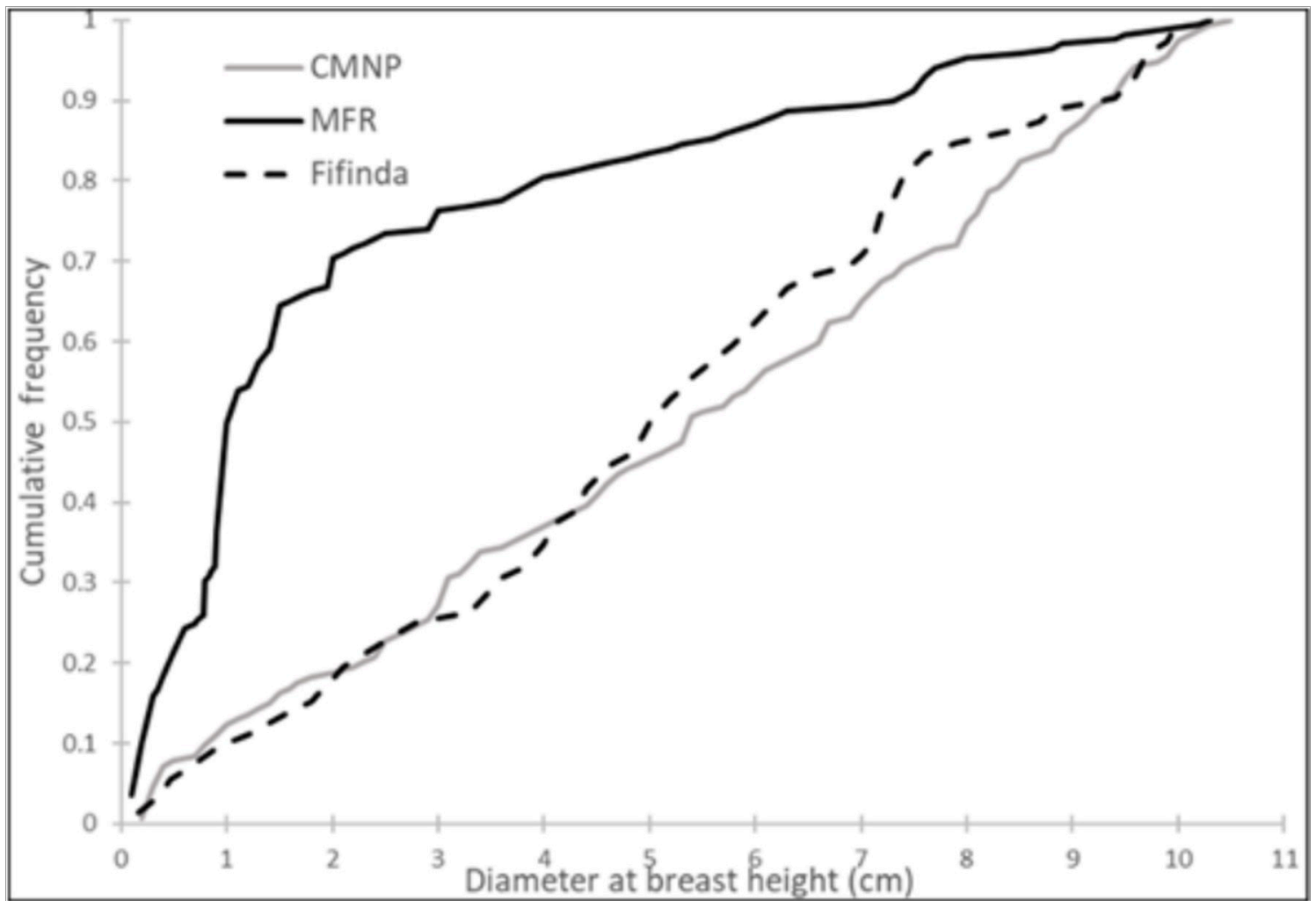


Figure 5

Cumulative relative frequency of juveniles (DBH < 10.6 cm) with diameter in different populations of *Coula edulis*