



Schinus terebinthifolia Raddi: a comparative framework on population genetic structure in a restored area after 12 years

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Received: 3 October 2021 / Accepted: 26 March 2022 / Published online: 18 April 2022
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Abstract The success of restoration projects depends on the genetic diversity of the implanted species. It is a limiting factor, often because the seed sources are immersed in highly fragmented landscapes. In this work, we compare the genetic diversity of the juveniles, and the adult trees of *Schinus terebinthifolia* Raddi in a native mixed-species planting, both in the restoration process and in the remaining natural vegetation Atlantic Forest Biome. Polymorphic DNA fragments using five SSR primers were used to estimate the restored population that showed a higher genetic diversity index (H_e) (0.553 adults and 0.505 juveniles) compared to the wild population

(0.487 adults and 0.483 juveniles). The forested area was established with individuals of high genetic diversity. There is a reduced genetic diversity for juveniles, with the loss of exclusive alleles and maintenance of endogamy and coancestry in reforested populations, and we can infer that there was a low gene flow inter fragments. The effective population size in both (adults and juveniles) was lower than the value recommended for the sustainability of populations in the short and long term. The results indicated that continuous monitoring of this particular area is of absolute necessity and should use techniques that promote the connectivity of the fragments. It would allow for a more significant reduction of genetic drift and the persistence of the planted populations.

Part of Doctoral Thesis of the first author.

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Keywords Inbreeding · Restoration monitoring ·
Pink pepper · Effective size

Introduction

The exploitation of natural resources in an unsustainable way has resulted in a reduction in the number of forested areas in the different biomes of Brazil. The sum of all native forest fragments above 100 ha corresponds to 8.5% of the original coverage of Atlantic Forest remnants (biodiversity hotspot), according to the latest SOS Mata Atlântica Report (2016). This scenario can be further disturbed since 72% of the Brazilian population lives within this biome domain.

However, actions are being developed as compensation strategies to mitigate the damages caused by anthropic activities on the forest's composition. Increasing the forest area through forestation and plantations is an important priority. It can be cited, as an example, that the Pact for the Restoration of the Atlantic Forest aims to recover 15 million hectares of forest by the year 2050 (Rodrigues et al. 2011; de Siqueira et al. 2021). Restoring degraded areas is an effective strategy to reestablish the forests' environmental services, including global warming mitigation by carbon sequestration. Restoring lands is especially important in the Atlantic Forest, a global hotspot in Brazil threatened by deforestation. It is necessary to apply the most suitable method for each situation to restore the degraded lands successfully. However, studies comparing restoration techniques are scarce. This lack of information hampers the Atlantic Forest restoration and, given the original complexity of its ecological dynamics (Zanini et al. 2021). However, many seeds and seedlings are necessary for projects to thrive.

The seeds collected for seedlings production aiming restoration projects must originate from these populations, along with reasonable levels of genetic variability and a minimal amount of endogamy (Sebbenn et al. 2003; Mesas et al. 2021). Genetic variability can play a decisive function in the survival of a species, especially when there is an unexpected alteration of the environment, it will then become increasingly important as a determinant of the actions of ecological restoration success (Sebbenn 2002; Vencovsky and Crossa 2003; Rodrigues et al. 2009; Mijangos et al. 2015; Lilian et al. 2021). Thus, new restoration projects may also need to consider the recuperation of genetic diversity and the regeneration of floristic diversity. The objective is to achieve the new population establishment (Kageyama and Gandara 2004; Rodrigues et al. 2009; Grelle et al. 2021).

Among the 17 States within the territorial limits of the Atlantic Forest of Brazil, the state of Sergipe is the most fragmented, with less than 50 ha (Sergipe 2014). The seed supplying from native species, as part of the forest restoration projects in the State of Sergipe, is often complex due to the low number of individuals with seeds present in any fragment. The action is considered to be within the necessary reliable distances for sampling. Consequently, the few genotypes represented in the lots of seeds may produce seedlings of related

individuals as full-siblings, half-siblings, and siblings of self-fertilization forest seedlings, thus resulting in endogamy (Álvares-Carvalho et al. 2017).

Although some natural populations of *Schinus terebinthifolia* in the State of Sergipe present high levels of genetic diversity, these are in decline due to a recent genetic bottleneck. It contributes to reduced genetic diversity in the future via increased endogamy (Álvares-Carvalho et al. 2015). This scenario, an alternative to maintaining the species' genetic heritage, is in forestation projects, associated with a potential to recover the degraded areas. The species *Schinus terebinthifolia* Raddi (pink pepper—Anacardiaceae) has environmental and socio-economic importance for its regions of natural occurrence in Brazil. It is a pioneer species, being dioecious, diploid, with a cross-pollinating strategy (allogamy) that depends upon biotic agents, such as bees, flies, and wasps (Lenzi and Orth 2004; Izoton et al. 2021).

The species is commonly used in restoration projects due to its plasticity and rusticity. The fruits in culinary are denominated poivre rose, also called aroeira or pink pepper, are appreciated as a condiment in the national and international marketplace. The extractivism of fruits of aroeira contributes to 20% of the income of the communities of fishermen in natural populations in riparian areas (Jesus and Gomes 2013). However, fruit harvesting in a non-sustainable way implies, over the years, a reduction in the number of regenerants. Consequently, compromising the genetic structure and the self-sustainability of the natural populations occurs. The fruits used mainly by the local extractivist for collection are sold to agroindustries in other states and are our primary source for seedling in the recovering degraded areas and ecological restorations. Being a pioneering fast-growth species produces flowers and fruits early, accelerating natural regeneration processes in its implanted areas. Therefore, this work was carried out to evaluate the adult and juvenile individuals of *S. terebinthifolia* and the diversity scenarios in reforestation with native mixed-species plantings in the Atlantic Forest area after 12 years of implantation.

Methods

Plant germplasm collection

The young leaves were collected from 309 individuals of *S. terebinthifolia* that were distributed in two populations: one, in mixed-species reforestation (Reflo) and another one, in a natural fragment (Nat), both located in an area of the Atlantic Forest, in the State of Sergipe, Northeastern Brazil.

The reforested area (Reflo) is a private property belonging to the Votorantim Cimentos S.A. (Cimentos Sergipe S.A.—CIMESA) Company, in the municipality of Laranjeiras (10S 48' 22" and 37W 10' 18"). The Northern and Eastern areas are fragments of native vegetation (Semidecidual and Mangrove Seasonal Forest). In 2005, this reforestation was carried out in a previously cultivated area with sugar cane crops with a conventional agriculture system. The native species reforestation was implanted using a model of quincunx system (four pioneer species and one central climax species), with 34 native Atlantic Forest tree species of different ecological groups. In the Reflo population, a census was accomplished in eight plots (30 m×20 m, each), where a total of 82 adults (implanted individuals) and 121 juveniles (regenerants) were identified and had their biological material collected for this study.

The second area (Nat) is a natural fragment in the Northern region of the State of Sergipe, in the municipality of Neópolis (10S 16' 37.80" and 36W 42' 28.79"). This fragment belongs to the Permanent Preservation Area (PPA), on the banks of the main river of the Brazilian Northeast, the São Francisco River. The sampling of the Nat population was achieved in a plot with 50 m×50 m, with 74 adults and 32 juveniles. For the juvenile stadium of this population, a height of up to 2 m was adopted. Geographical coordinates of all individuals were addressed via the Global Positioning System (GPS). The individuals were evaluated for their diversity with Simple Sequence Repeat (SSR) markers. DNA of the leaves was obtained by the optimized CTAB method, with 0.2% of 2-mercaptoethanol (v/v) (Nienhuis et al. 1995).

Genotyping

The DNA fragments of all individuals were amplified in a Thermocycler using five nuclear microsatellite sequences (Saat 09, Saat 17, Saat 25, Saat 47, and Saat 55) (Williams et al. 2002). The total volume of each amplified sample corresponded to 12.0 µL: 2.0 µL of DNA (5 ng µL⁻¹) was added to 10.0 µL of the reaction mix [1.3 µL of 10× PCR buffer (10 mM Tris–HCl pH 8.3, 50 mM KCl), 1.0 µL dNTP (2.5 mM), 0.2 µL Taq polymerase (Ludowig) (1 U) and 1.0 µL each primer (2 µM). The final volume was completed with ultrapure water].

Reactions for the DNA amplification were performed on GenePro Bioer Technology Thermocycler. Thirty-five cycles of amplification, consisting of a 5 min initiation step at 94 °C, with denaturation at 94 °C for 1 min, annealing at a consistent temperature for each of the five SSR primers for 40 s, with an extension at 72 °C for 1 min. At the end of this stage, an extension occurred at 72 °C for 10 min.

The amplified products were separated by electrophoresis in an 8% polyacrylamide gel at 130 V, 20 mA, and 2 W for 3 ½ hours. After the electrophoresis, the gel was stained with silver nitrate (0.2% AgNO₃) and developed with a 3% HNO₃ solution and formaldehyde (60 µL 100 mL⁻¹ of 3% HNO₃ solution), and 20 bp and 100 bp ladders were used.

Data analysis

The observed heterozygosity (Ho) and the expected heterozygosity (He) (genetic diversity of Nei 1978) were estimated using GenAlEx Software Version 6.2 (Peakall and Smouse 2012). The inbreeding coefficient, inferred from the estimation of the fixation index (F) (Weir and Cockerham 1984), as well as the allelic richness (AR), were both obtained with FSTAT Software Version 2.9.3.2 (Goudet 1995). The genetic data were obtained for both adults and juveniles.

Based upon the number of individuals sampled (n), the coancestry coefficient (Fij) and the fixation index of each population (F), together with the inbreeding effective population size for adults and juveniles, were based on Sebbenn and Seoane (2005):

$$N_e = 0.5n / \left[(1 + F) * \left(0.5n + \sum n_x = 1 \sum n_y \neq 1 \theta_{xy} \right) \right]$$

N_e = the inbreeding effective population size; n = the number of individuals from each population; F = the coefficient of inbreeding, inferred from the estimation of the fixation index; and $\sum x = 1 \sum y \neq 1 \phi_{xy}$ = the sum of all of the coancestry among the pairs of individuals of each population.

The coancestries were inferred from the kinship coefficients (Loiselle et al. 1995) with SPAGeDi 1.2 (Hardy and Vekemans 2002). The genetic representativity (N_e/n) of each sample was also estimated.

The minimum viable population (MVP) for the in situ genetic conservation was estimated by the equation proposed by Silva and Pinto (2009): $PMV = N_{ref} * n / N_e$. N_{ref} = the effective population size of the reference; n = the sample size, and N_e = the effective population size. Effective reference sizes of 150 individuals and 1,000 individuals were used for the long and short-term conservations, respectively (Sebbenn 2006; Frankham et al. 2014).

Results

When comparing the populations' allelic richness (AR), the Reflo area was superior. The Nat population presented higher Ar values in the juveniles (3.082) and the Reflo adults (4.343). The Nat and Reflo populations, for those individuals in the juvenile stadium, presented exclusive alleles. Only the Reflo population showed complete alleles (three) (Table 1).

Reflo population presented a higher genetic diversity ($H_e = 0.553$ and 0.503 for adults and juveniles, respectively) than the Nat population ($H_e = 0.487$ and 0.483 for adults and juveniles, respectively). The adults and juveniles from the Nat population presented low fixation indexes (F), which were not significantly different from zero, which allowed us to infer an absence of inbreeding. The values (F) in the Reflo population were high, 0.310 in adults and 0.261 in juveniles (Table 2).

For adults, the Nat population showed a negative consistency coefficient ($F_{ij} = -0.035$), contributing to the absence of population genetic structuring. Reflo population presented a consistency coefficient of 0.338 , indicating that the population means for the studied loci were full-siblings. For the juvenile stadium, Nat population had a $F_{ij} = 0.105$ (half-siblings) and for Reflo had a $F_{ij} = 0.284$ (full siblings) (Table 3).

The distribution of the individuals by distance class was observed in Nat (natural) population, the adults presented a degree of kinship of half-siblings in the first and second classes ($F_{ij} = 0.186$ and 0.150). From the distances of 10.77 m, the values of F_{ij} were reduced. The juveniles of this population presented F_{ij} of 0.112 and 0.115 in the first and third distance classes, respectively. The adults of Reflo (reforested) showed F_{ij} of 0.374 and 0.092 in the first and second distance classes, respectively (up to 170.70 m), and the juveniles presented F_{ij} of 0.303 (full siblings) and 0.034 , respectively (Fig. 1).

Nat population presented individuals with a higher genetic representativeness (adults = 1000 and juveniles = 0.967), compared to Reflo population (adults = 0.757 and juveniles = 0.789).

Discussion

The highest rates of genetic diversity for the reforested (Reflo) population of *S. terebinthifolia* indicated that the area was established through individuals with high genetic diversity. These values of diversity were higher than those observed for the same species in eight natural fragments in the states of Minas Gerais ($H_e = 0.25$), Espírito Santo ($H_e = 0.37$), and Sergipe ($H_e = 0.24$ and 0.49) (Álvares-Carvalho et al. 2016). Despite the high genetic diversity index introduced in the Reflo area, reduced diversity among the juveniles was observed. Thus it results in the number of exclusive alleles, which leads to the loss of interest in the alleles, mainly those related to resistance, biotic stresses, and abiotic matter. This reduction of genetic diversity may result from the low gene flow among the fragments of the environment, contributing to the non-random crossing of the individuals; consequently, to the maintenance of endogamy and coancestry in the Reflo population.

When studying natural and reforested areas with the *Inga vera*, it was observed that even with the implantation of individuals with high genetic diversity, the juveniles presented an inbreeding coefficient equal to $F = 0.303$. The authors asserted that habitat fragmentation could alter the reproductive strategies in plant communities and negatively interfere with the plant-pollinator interactions, favoring the dispersal of pollen grains at a closer range. These changes may increase an inbreeding situation, leading to the

Table 1 Frequencies of the alleles in the microsatellite loci of *Schinus terebinthifolia* Raddi in different populations and at different stadiums of development

Locus		Populations			
		Nat adults	Nat juveniles	Reflo adults	Reflo juveniles
	<i>N</i>	74	32	82	121
Saat 09	(<i>n</i>)	67	23	72	103
	1	–	–	0.083	0.150
	2	–	–	0.410	0.345
	3	0.500	0.500	0.417	0.398
	4	0.500	0.500	0.090	0.078
	5	–	–	–	0.029
Saat 17	(<i>n</i>)	65	31	71	93
	1	–	–	0.077	–
	2	–	–	0.106	–
	3	–	–	0.127	0.086
	4	–	–	0.042	0.032
	5	0.600	0.258	0.380	0.462
	6	–	–	0.014	–
	7	0.400	0.742	0.254	0.419
Saat 47	(<i>n</i>)	66	30	74	105
	1	0.152	0.067	0.095	0.090
	2	0.470	0.367	0.865	0.857
	3	0.379	0.517	–	0.033
	4	–	0.033	0.041	0.019
	5	–	0.017	–	–
Saat 55	(<i>n</i>)	69	29	73	119
	1	–	–	0.123	0.067
	2	0.877	0.810	0.678	0.790
	3	0.123	0.190	0.199	0.143
Saat 25	(<i>n</i>)	71	32	80	117
	1	0.007	–	0.025	–
	2	0.021	–	0.081	0.051
	3	0.394	0.453	0.344	0.274
	4	0.063	0.047	0.044	0.094
	5	0.049	0.094	0.481	0.547
	6	0.007	0.016	–	–
Natural (Nat), Reforested (Reflo), the total number of individuals sampled (<i>N</i>), and the number of heterozygous individuals (<i>n</i>)	7	0.458	0.391	0.025	0.034
	N. total alleles	16	16	23	21
	N. exclusive alleles	0	1	3	1

crossing between related individuals (Cruz Neto et al. 2014; González et al. 2020).

The adult and juvenile individuals of Nat population did not present spatial genetic structuring from a distance of 10.77 m, and they were not related from this distance. This finding may be associated with pollinators and dispersers in the area. It contributes to

a better distribution of the alleles and the genotypes, maintaining the genetic diversity (H_e). The adults of Reflo population were planted during the reforestation project, so this genetic structure in distance class was not natural.

In the juveniles of Reflo population, relatives (full-siblings, $F_{ij}=0.284$) were observed in the first

Table 2 Mean indexes of the genetic diversity for the five microsatellite *loci* of *Schinus terebinthifolia* Raddi were located in the different populations and at the different stages of development

	A_R		H_o		H_e		F	
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
Nat	2.851	3.082	0.501	0.478	0.487	0.483	−0.021	0.027
Reflo	4.343	3.953	0.385	0.374	0.553	0.503	0.310*	0.261*
Mean	3.597	3.518	0.443	0.426	0.520	0.493	0.145	0.144

A_R allelic richness; H_o observed heterozygosity; H_e expected heterozygosity (genetic diversity of Nei); F the coefficient of inbreeding, inferred from the estimation of the fixation index

*Significant at a 5% of probability

Table 3 Sample size (n); the effective population size (N_e); the relationship between the effective population size and the sample size (N_e/n); the minimum viable population with the effective reference size MVP ($N_{e_{ref}}=150$); MVP ($N_{e_{ref}}=1000$); and the coancestry coefficient (F_{ij}) of the natural populations (Nat) and the reforested populations (Reflo) of *Schinus terebinthifolia* Raddi

Parameters	Stadiums of development	Populations	
		Nat	Reflo
n	Adults	74	82
	Juveniles	32	121
N_e	Adults	74.00	62.08
	Juveniles	30.95	95.50
N_e/n	Adults	1.022	0.757
	Juveniles	0.967	0.789
PMV ($N_{e_{ref}}=150$)	Adults	146.71	198.13
	Juveniles	155.08	190.05
PMV ($N_{e_{ref}}=1000$)	Adults	978.06	1320.87
	Juveniles	1033.92	1267.01
F_{ij}	Adults	−0.035	0.338
	Juveniles	0.105	0.284

distance class (14 m), which was close to that found in the natural area. Although pollinators and dispersers may have occurred in the reforestation area, this supply may not have been enough, as there was still a solid genetic structuring of the juveniles and a loss of gene diversity (H_o , H_e and AR). Another factor contributing to the spatial genetic structuring in the dioecious species was individuals of one sex in a high level in the area, providing directed crossings and, consequently, related offspring.

The effective population size (N_e) inferred the effects of genetic drift in each population at different stadiums of their life. The adults in the Nat population

do not suffer genetic drift. Thus, the 74 individuals corresponded to an ideal population (panmictic), with random crossings, without selection, migration, mutation, kinship and endogamy (Sebbenn and Seoane 2005, Sujii et al. 2021). Endogamy and coancestry altered the N_e in the juveniles, even at a low level. In the Reflo population, the effect of genetic drift was lower than in the juveniles, inferring that if all had reached a fertile stadium, the genetic representativity of the individuals would have been 78.9%. The values found in the present study were higher than those found in studies in the natural areas of the Atlantic Forest, of the Caatinga, and the Ecotone regions of the state of Sergipe. Estimative of 23, 15, and 42 of N_e , were obtained in these regions. These determinations have allowed us to infer that they represented 50% of an ideal panmictic population (Álvares-Carvalho et al. 2015, Martins et al. 2021), implying the necessity of preserving populations.

The relationship between the effective size (N_e) and the sample size (N) is essential in planning conservation strategies. A balance considering demographic events, such as the temporal fluctuations in population size, the presence of structure and the inbreeding, the differences in infertility, as well as the asynchronous flowering, the N_e were very close to the number of individuals that were collected (Loveless and Hamrick 1984, Hamann 2004). Reflo population presented a higher relationship in juveniles due to their lower values of coancestry and inbreeding than adults.

Based on the values recommended for conserving populations in short ($N_e \geq 150$) and long periods ($N_e \geq 1000$), both populations need conservation strategies to maintain their genetic diversity and contain the effects of genetic drift. In a study

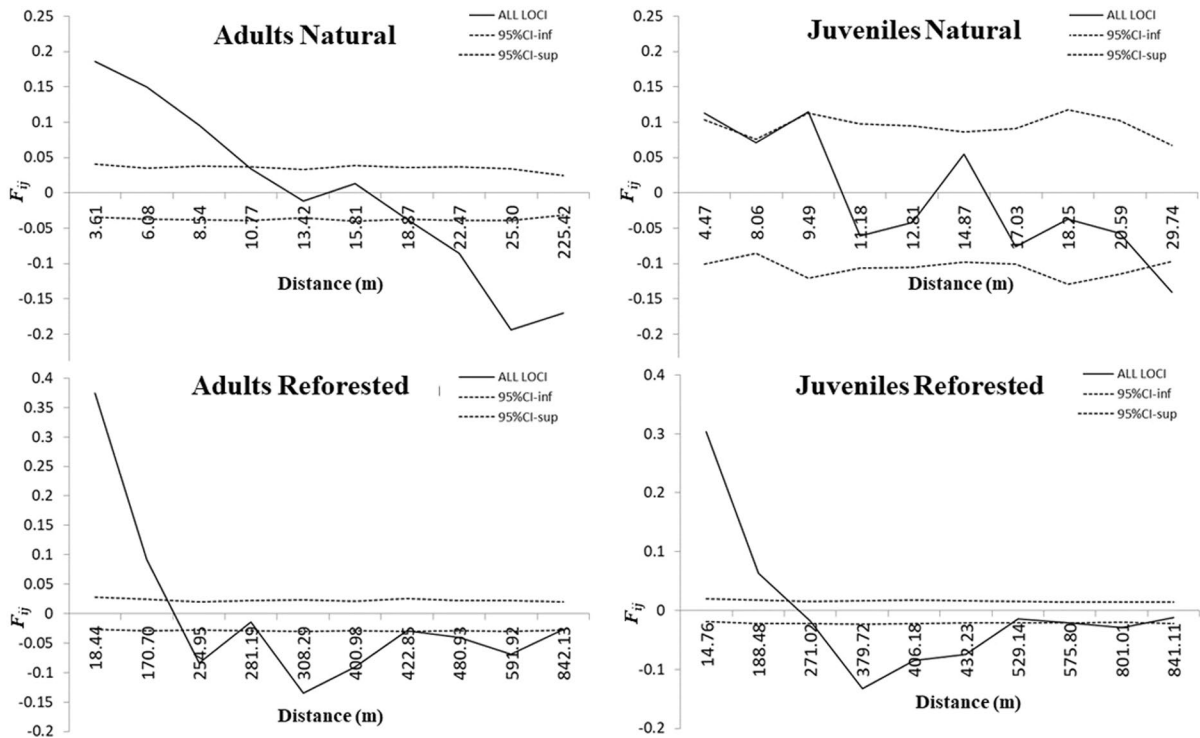


Fig. 1 Correlograms of the coancestry coefficient (F_{ij}) of *Schinus terebinthifolia* Raddi, by distance, in Nat (natural) and Reflo (Reforested) populations, at the different stadiums of

development. The dashed lines represent the confidence intervals, at a 95% of probability

with *Centrolobium tomentosum*, a native species from Atlantic Forest pollinated by bees, the adverse effects of inbreeding on the population's effective size in adults' and juveniles' natural remnants the restoration areas were observed. The authors attributed those facts to the small population sizes associated with the spatial genetic structures and deficit of pollination service (Sujii et al. 2017).

It is essential to increase the gene flow among the fragments around the reforested area, allowing the maintenance of the genetic diversity of the individuals implanted throughout the generations and, consequently, the generation of self-sustainability of the generations settlement. An alternative would be installing new reforestation projects based on fragments. It is essential to improve the gene flow among the fragments around the reforested area, permitting the maintenance of the genetic diversity of the individuals implanted throughout the years and, consequently, the self-sustainability of the generations settlement. The reforested area will serve

as a seed supplier for future reforestation projects in the Atlantic Forest area through these efforts.

Acknowledgements We thank the National Council for Scientific and Technological Development—Brazil (CNPq), the Coordination for the Improvement of Higher Education Personnel—Brazil (CAPES), Federal University of Sergipe, and the Research Group on Conservation, Breeding and Management of Genetic Resources (GENAPLANT).

Author contributions EMSS conducted the research and wrote the text, RSM and RAF guided the research, revised the text and contributed to the writing of the manuscript, SVAC contributed to obtaining the research data, in the writing and revision of the text. All authors contributed to the article and approved the submitted version.

Funding This study was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior [Grant No. 001], Conselho Nacional de Desenvolvimento Científico e Tecnológico.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest All the authors of this manuscript declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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