Universidade Federal de Goiás
Instituto de Ciências Biológicas
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O papel da estrutura da paisagem na variabilidade genética da palmeira Euterpe edulis na Mata Atlântica

Carolina da Silva Carvalho

Orientador: Rosane Garcia Collevatti
Co-orientador: Milton Cézar Ribeiro

Goiânia
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Sumário

Estrutura da dissertação

Essa dissertação está estruturada em dois capítulos cujo objetivo geral foi entender como características da paisagem influenciam a variação e a estruturação genética, usando a abordagem de genética da paisagem e a palmeira *Euterpe edulis* (Arecaceae) como modelo de estudo. A genética da paisagem surgiu a partir da junção de três grandes áreas da ciência: ecologia da paisagem, ecologia espacial e genética de populações (Manel et al. 2003). Difere-se de disciplinas clássicas como genética de populações e filogeografia, pois incorpora testes explícitos de heterogeneidade ambiental a fim de entender a distribuição da variabilidade genética no espaço (Storfer et al. 2007).

Dentre as abordagens frequentemente realizadas na genética da paisagem podemos: identificar características da paisagem que influenciam a conectividade e diversidade genética, realizar design de corredores ecológicos e reservas, e predizer impactos de futuras mudanças ambientais na conectividade e permanência da espécie (Spear et al. 2010). No entanto, a primeira abordagem é a mais utilizada nos estudos, onde são testados o efeito do relevo, da hidrografia, das estradas (Spear et al. 2005), dos corredores, do tamanho e do isolamento dos fragmentos, e da proporção de habitat (Coulon et al. 2004, Dixo et al. 2009) sobre o fluxo gênico e variação genética. Além disso, a genética da paisagem pode ser particularmente importante para explicar padrões originados a partir de processos micro-evolutivos (Manel et al. 2003), principalmente em paisagens extremamente fragmentadas.

Como é uma área relativamente nova, estudiosos da genética da paisagem vem colocando esforços para testar uma grande variedade de métodos estatísticos (e.g. Cushman et al. 2006, Cushman & Landguth 2010, Wagner & Fortin 2012), técnicas de tratamento espaciais de dados, e favorecendo-se da alta tecnologia do desenvolvimento de marcadores genéticos (Spear et al. 2005, Storfer et al. 2007). No entanto, apesar do crescente número de publicações, Storfer e colaboradores (2010) encontraram que a maioria dos estudos em genética da paisagem ainda está concentrada na América do Norte e Europa, sendo que 90% dos estudos incluem apenas uma espécie e apenas 14,5% desses é realizado com plantas.

Portanto, no primeiro capítulo dessa dissertação intitulado “Linking genetics to landscape: large scale study of an Atlantic Rainforest palm species *Euterpe edulis*” foi realizada uma metanálise com o objetivo de avaliar a contribuição relativa da heterogeneidade ambiental, da adequabilidade ambiental para o estabelecimento da espécie, e dos efeitos antrópicos para explicar a variação da diversidade genética e do grau de endocruzamento em populações de *Euterpe edulis* ao longo do bioma Mata Atlântica. O segundo capítulo intitulado: “Matrix resistance and habitat loss determines patterns of genetic differentiation in a Rainforest palm species”, avaliou se a perda de habitat e a fragmentação afetam a variabilidade e diferenciação genética do *E. edulis*. Para responder a nossa pergunta, sete paisagens de 2 km foram analisadas no estado de São Paulo, sudeste do Brasil, totalizando 22 áreas. Para acessar a variabilidade e diferenciação genética dessas áreas, utilizamos 8 locos de microssatélites e usamos comparação de modelos com múltiplas hipóteses concorrentes baseado no critério de informação de Akaike (AIC).

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CAPÍTULO 1

LINKING GENETICS TO LANDSCAPE: LARGE SCALE STUDY FOR A ATLANTIC RAINFOREST PALM SPECIES *Euterpe edulis*

Title: Linking genetics to landscape: large scale study of an Atlantic Rainforest palm species *Euterpe edulis*

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Abstract

Understanding how environment heterogeneity and humans impacts affect the genetic variability in large scale is essential to species management planning. However, most studies in conservation genetics are carried out in local or regional scale, and rarely in broad spatial scales such as the entire biome. Using meta-analysis, we evaluated the relative contribution of environmental heterogeneity, habitat suitability to the establishment of the species, and human footprint to explain genetic diversity (H_e), number of alleles (A) and inbreeding (F_{IS}) variation among populations, using *Euterpe edulis* (Arecaceae) as a model species and the Atlantic Rainforest as model system. Analyses were based on multiple competing hypotheses approach with model selection based on Akaike's Information Criteria (AIC). Models were fitted using Generalized Addition Models (GAM), and Generalized Linear Models (GLM). Inbreeding was best explained by habitat suitability whereas number of alleles was explained by latitude, a surrogate of habitat heterogeneity, and H_e by the distance from the Atlantic Ocean coast (related to human footprint), forest type (habitat heterogeneity) and percentage of forest cover (human footprint). Therefore, our results show that environmental heterogeneity, habitat suitability and human footprint are essential to explaining de genetic variability in *E. edulis.*

Introduction

Understanding how environmental heterogeneity and human footprint affect patterns of biodiversity distribution and maintenance is a challenge for both ecologists and biogeographers (Gaston 2000). Although biological diversity encompasses from genes to ecosystems, few studies have reported the role of environmental heterogeneity and human footprint in genetic variability in a broad scale (e.g. Diniz-Filho et al. 2009, Ortego et al. 2012). Understand the distribution of genetic variability is extremely important for species viability analysis (Hughes et al. 2008), once species that show very low genetic variability may have low potential to adapt to environment changes and become endangered or face extinction (Hoffmann & Willi 2008).

Landscape genetics plays an important role in species conservation planning, because it allow us to quantify the relative contribution of landscape structure variables to explain genetic variability and connectivity among populations (Segebacher et al. 2010, Spear et al. 2010, Sommer et al. 2013). This includes a set of variables, such as the relief, hydrographic system (e.g. Spear et al. 2005), roads (e.g. Frantz et al. 2012), ecological corridors (e.g. Munshi-south et al. 2012), habitat amount, patch size and isolation (e.g. Coulon et al. 2004, Dixo et al. 2009, Lange et al. 2012).

Studies in multi-scale, from local to large scale, are also important to better understand biodiversity distribution and contribute for efficient species conservation planning (Huber et al. 2010). However, studies that report the role of environmental heterogeneity and human footprint in genetic variability are frequently carried out at local or regional scales, and rarely at address the effects at large scales, such as entire biomes (but see Diniz-Filho et al. 2009, 2012, Collevatti et al. 2011, Ortego et al. 2012).

Meta-analysis may contribute in those cases by combining studies carried out at different scales, and generalizing them to understanding large scale patterns (e.g. Lowe et al. 2005, DiBattista 2008). Despite the increasing in meta-analysis works in ecology field, this approach is still uncommon in conservation genetics studies. The few studies published so far focused in only one or few variables of environmental heterogeneity and human footprint in attempt to explain genetic variability patterns due to habitat loss or

fragmentation (e.g. Honnay & Jacquemyn 2007, Aguilar et al. 2008, Vranckx et al. 2011), and few studies deal with many variables to describe the environmental features (e.g. Ortego et al. 2012).

Atlantic Rainforest is one of the 25 world's hotspots of biodiversity (Mittermeier et al. 2005). Due to its wide geographical distribution, it is highly heterogeneous in climate, relief and vegetation type (Mittermeier et al. 2005, Ribeiro et al. 2011). However, it is also one of the most threaten ecosystem in South America mainly due to anthropic disturbance (Butchart et al. 2010, Tabarelli et al. 2010), and nowadays it is reduced to 11.7% of its original 150 millions of hectare (Ribeiro et al. 2009). Thus, Atlantic Rainforest is a good model system to understand the role of environmental heterogeneity and human footprint in genetic variability. The heart of palm (*Euterpe edulis,* Arecaceae), an Atlantic Rainforest threaten species (MMA 2008), was once one of the dominant palms in this ecosystem (Henderson et al. 1995), present in different types of vegetation, from dense mountain rainforests to seasonally dry forests, where it is restricted to wet microhabitats. The edible meristem (heart of palm) obtained mainly by illegal extractivism is used as source of raw material for food industries (Galetti & Fernandez 1998), and the ripened fruits are consumed by many species of birds and mammals (Galetti & Aleixo 1998).

In this study we evaluated the relative contribution of environmental heterogeneity, habitat suitability to permanence and establishment, and human footprint in explaining the genetic variability using *E. edulis* as a model species. We expect that human footprint reduces genetic variability due to the disruption in ecological processes such as seed dispersal and pollination (e.g. Fahrig 2003, Aguilar et al. 2008, Uriarte et al. 2011). Also, overexploitation, habitat fragmentation, and population isolation may affect population effective size, causing bottlenecks and decreasing gene flow and genetic variability (Young et al. 1996). Nevertheless, higher environmental heterogeneity and habitat suitability, may lead to an increase in genetic variability, as low habitat suitability may decrease population size and, potentially, genetic variability (e.g. Garner et al. 2004, Diniz-Filho et al. 2009).

Methods

Literature search

We surveyed the literature for population genetic studies of *E. edulis* in Scielo, Web of Science, Scopus, and Google Scholar. All published information available up to June of 2012 was included in our analysis. We obtained five publications that accounted for 44 study sites (Supplemental Information Table S1). Moreover, we used our own unpublished data for additional 23 study sites summing up 67 sites. However, four sites were excluded from the analysis because they were outside the Atlantic Rainforest biome, and finally we used 63 sites. We identified four different types of molecular markers in the studies: AFLP, isoenzymes, aloenzymes and microsatellites. The spatial distribution of study locations extends from Bahia state to Rio Grande do Sul state (Fig. 1 and Supplemental Information Table S1).

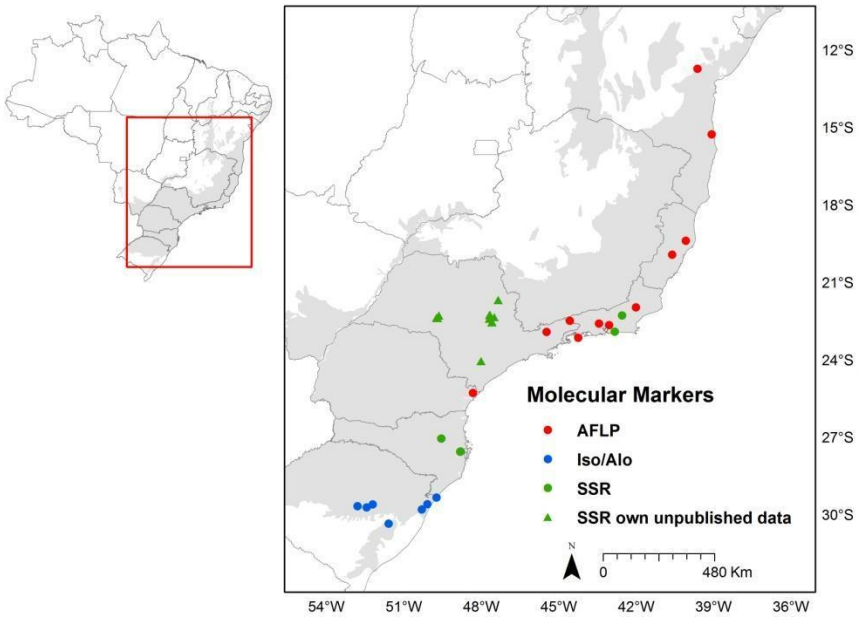

Fig. 1: Distribution of the 63 study sites with genetic information for *Euterpe edulis* across the Brazilian Atlantic Rainforest biome in Brazil. The different molecular markers methods are highlighted. Iso/Alo= Isoenzymes and Aloenzymes, SSR= Microsatellites, and AFLP= Amplified Fragment Length Polymorphism.

Genetic variability response variables

Three genetic parameters were used as response variables in our meta-analysis: the inbreeding coefficient (F_{IS}); the genetic diversity, measured by expected heterozygosity (*He*) and the number of alleles per loci (*A*). We chose these genetics parameters because they are present in most publications (Supplemental Information, Table S1), and are frequently used in conservation genetics studies as surrogates of population evolutionary potential (Frankham et al. 2008). Because F_{IS} cannot be estimated using dominant molecular markers, such as AFLPs, we excluded those studies from the analyses of inbreeding.

Predictive models

To analyze the effect of landscape features on genetic variability, we first removed the effect of molecular markers from original genetic data using General Linear Model (GLM) (Supplemental Information Fig. S1, S2 and S3). The residuals were then used as response variables for the next steps of analysis.

Three groups of predictive variables were used in order to explain genetic variability (Fig. 2): (i) landscape structure and human-footprint; (ii) environmental heterogeneity and (iii) habitat suitability. Landscape structure and human-footprint predictors were: a) percentage of forest cover, b) defaunation (binary variable, 0=not defaunated and 1=defaunated), c) functional connectivity, d) distance from the Atlantic Ocean coast, and e) date of settling. Environmental heterogeneity was measured by forest type (seasonally dry forest and rainforest), facing slope, declivity and latitude. Habitat suitability to permanence and establishment of the species was measured by drainage density, habitat suitability, and distance from the locality with highest habitat suitability. We also included a null model considering the absence of landscape features effect as an alternative hypothesis.

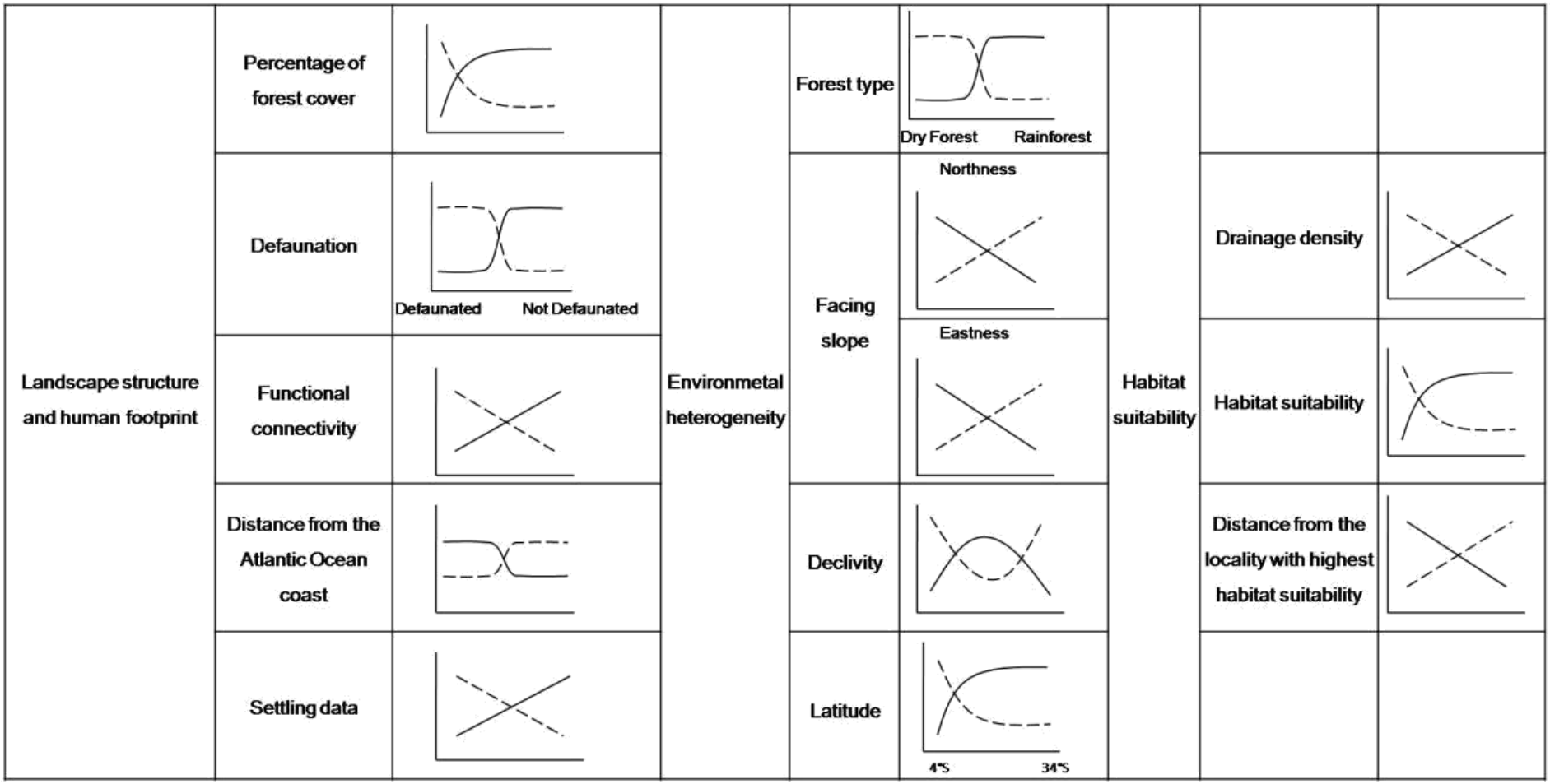

Fig. 2: Prediction of the relationship between each genetic parameter and compete models. The dashed line represents the expected for inbreeding coefficient (F_{IS}) and the continuous line the expected for genetic diversity (H_e) and number of alleles per loci (A).

To estimate the predictive variables we drew a buffer with 20 km of radius in each of the 63 sites. Percentage of forest cover was calculated using the SOS Mata Atlântica map (2005). For this, we calculated the total area of forest inside each buffer of 20km and the percentage using the software ArcGIS 9.2 (ENRI). Defaunation status was defined as a binary variable for each site: defaunated (1) or non-defaunated (0). The areas were considered defaunated when there were no records of Ramphastidae species in the buffer area. Species of this family are important long distance dispersers for *E. edulis* (Holbrook 2011, Galetti et al. 2013). To classify the sites we searched the wikiaves website (www.wikiaves.com.br) and also referred a specialist in frugivory and seed dispersal (M. Galetti, pers.comm).

Functional connectivity is a measures of how easy is the biological flow in a specific landscape (Taylor et al. 1993), taking into account the capacity of individuals to move from one place to another (Uezu et al. 2005, Awade & Metzger 2008, Boscolo et al. 2008 Metzger et al. 2009). The functional connectivity was calculated as the dispersal distance of a Ramphastidae species (450 m, Holbrook 2011). Based on this functional group, we draw a buffer of 300 meters in each forest remnant, using the SOS Mata Atlântica map (2005), and calculated the total area of functionally connected forest using the software ArcGIS 9.2 (ENRI).

The distance from each site to the Atlantic Ocean coast was estimated using Euclidean distance using the software ArcGIS 9.2 (ENRI); and the settling date was estimated using the age of the city foundation where each site is localized. The settling date is a surrogate of the time-lag between the time of fragmentation and the genetic response to fragmentation.

For forest type, each site was classified categorically as rainforest or seasonally dry forest. Facing slope refers to the hillside facing, and it is indirectly related to the solar radiation that affects temperature and humidity. The North hillside is less favorable to the establishment of *E.edulis* because of the lower solar radiation received by the North facing slopes in the South Hemisphere. To calculate the facing slope, we used the digital map of elevation (http://edcdaac.usgs.gov/gtopo30/hydro/), using the software ArcGIS 9.2 (ENRI). Since the facing slope is a circular measure, we divided it into two variables: northness and eastness. The northness was calculate using the

formula cos(facing slope *π/180) and eastness using the formula sin(facing slope *π/180). Declivity was calculated also using the digital map of elevation with the software ArcGIS 9.2 (ENRI), and Latitude was represented by the latitudinal coordinate of each site.

Drainage density was calculated as the total amount of drainage in meters per hectare for each buffer of 20km using the software ArcGIS 9.2 (ENRI). It was estimated using the hydrography map of Agência Nacional de Águas – ANA (www.ana.gov.br).

For habitat suitability model, we modeled species ecological niche using Maximum Entropy method (Maxent, Phillips & Dudik 2008). Occurrence records (229) were obtained from Species Link (www.splink.org.br), Jardim Botânico do Rio de Janeiro (www.jbrj.gov.br) and Biota Fapesp. Five climatic variables obtained from WordClim (www.worldclim.org/bioclim) were used: Annual Mean Temperature (BIO1), Temperature Annual Range (BIO7), Annual Precipitation (BIO12), Precipitation of Wettest Month (BIO13), Precipitation of Driest Month (BIO14). We also used altitude and forest cover (SOS Mata Atlantica (2005) map). We used 30% of our data for evaluation model, that retrieved a high AUC (area under ROC- Receiver Operating Characteristics Curve) of 0.901, meaning that our model it is close to perfect discrimination (Phillips & Dudik 2008).

Further, we calculate the distance from the locality with the highest habitat suitability. We selected the areas with high size and habitat suitability higher than 0.8. Then we calculated the Euclidean distance from the locality with the highest habitat suitability selected to each study site. This analysis was made using the software ArcGIS 9.2 (ENRI).

For the null model, we generated a random dataset with normal distribution using R software (R Core Team 2012). We also analyzed the correlation among all variables (Supporting Information Table S2)

Statistical analyses

Each model was fitted using Generalized Addition Models (GAM - “gam” R package), except the two categorical variables (“forest type” and “defaunation”) that were fitted using Generalized Linear Models (GLM– “stat” R package). Because the effect of landscape in genetic variables tend to be

complex and dependent on the interaction of diverse factors (Boscolo & Metzger 2011), we used model selection with multiple compete hypothesis approach (Burnhan & Anderson 2002). To select the best model we used Akaike information criteria (AIC), where the model with lower AICc (AIC corrected by sample size and number of parameters, Burnhan & Anderson 2002) was considered as more plausible to explain observed patterns. AICc*i* (where *i* represents each model) was also calculated as the difference between AICc for the model *i* and the smallest observed AICc. Models with AICc<2 are equally plausible to explain the observed pattern (Zuur et al. 2009). Akaike's weight of evidence (wAICc) was obtained, representing the relative contribution of model *i* to explain the observed pattern, given a set of compete models (Burnhan & Anderson 2002). All analyses were performed with the function "ICtab()"of "bbmle" R package.

Results

Most populations of *E. edulis* showed high genetic diversity and polymorphism (Supplemental Information Table S1). For the 35 sites using microsatellite markers, H_e ranged from 0.72 to 0.85, and number of alleles (*A*) varied from 7.6 to 15.1. For isoenzymes/aloenzymes, H_e ranged from 0.2 to 0.45, and *A* from 2.0 to 3.4, and for AFLP, H_e ranged from 0.09 to 0.16. However, the inbreeding coefficient (F_{IS}) was also high in many populations, ranging from 0.04 to 0.31 for microsatellites, and from -0.16 to 0.22 for isoenzymes/aloenzymes (Supplemental Information Table S1).

Variation in H_e was best explained by distance from the Atlantic Ocean coast, forest type and percentage of forest cover (Table 1). Distance from the Atlantic Ocean coast was negatively related with genetic diversity (Fig. 3A), with a strong decrease in H_e after ~ 150 km from the coast. *Euterpe edulis* populations in rainforest showed higher genetic diversity, but populations in seasonally dry forests showed both, high and low genetic diversity (Fig. 3B). Moreover, sites with high percentage of forest cover tended to have high H_e (Fig. 3C), although some sites with low percentage of forest cover also presented high values of H_e.

Number of alleles (*A*) was best explained by latitude (Table 1), with higher number of alleles at intermediary latitudes (Fig. 4).

Variation in F_{IS} was most likely due to differences in habitat suitability (Table 1). Habitats with higher suitability tended to have lower F_{IS} (Fig. 5), although some sites with low habitat suitability also presented low values of F_{IS}.

Table 1: Model selection of the compete hypotheses used to explain the genetic variability pattern in population of *Euterpe edulis* from 63 sites, distributed along the Brazilian Atlantic Rainforest. K= number of parameters; H_e= expected heterozigozity; *A*= numbers of alleles; F_{IS}= inbreeding coefficient. Bold numbers show the best models for each genetic parameter.

Predictor models	H_e			*A*			F_{IS}		
	K	ΔAICc	wAIC	K	ΔAICc	wAIC	K	ΔAICc	wAIC
% Forest cover	3	4.6	0.03	3	13.0	<0.01	3	6.7	0.02
Defaunation	3	4.9	0.03	3	24.2	<0.01	3	4.6	0.06
Functional connectivity	3	4.6	0.03	3	11.2	<0.01	3	6.6	0.02
Distance from the Atlantic Ocean coast	3	**0.0**	**0.32**	3	7.1	0.03	3	8.9	0.01
Distance from the Atlantic Ocean coast + % Forest type	4	**1.7**	**0.14**	4	9.4	0.01	4	9.4	0.01
Distance from the Atlantic Ocean coast + % Forest cover	4	**2.2**	**0.11**	4	9.1	0.01	4	11.4	<0.01
Setting data	3	5.8	0.02	3	24.6	<0.01	3	5.9	0.03
Forest type	3	4.5	0.03	3	9.4	0.01	3	6.5	0.02
Northness	3	5.3	0.02	3	26.1	<0.01	3	4.8	0.06
Eastness	3	4.8	0.03	3	23.5	<0.01	3	6.1	0.03
Declivity	3	4.4	0.04	3	10.7	<0.01	3	6.6	0.02
Latitude	3	4.5	0.03	3	**0.0**	**0.93**	3	6.4	0.02
Drainage density	3	5.6	0.02	3	18.1	<0.01	3	6.0	0.03
Drainage density + % Forest cover	4	7.1	0.01	4	10.8	<0.01	4	8.3	0.01
Drainage density + Declivity	4	7.4	0.01	4	11.8	<0.01	4	8.7	0.01
Habitat suitability	3	2.3	0.10	3	17.0	<0.01	3	0.0	**0.60**
Distance from the locality with highest habitat suitability	3	6.0	0.02	3	10.2	<0.01	3	7.0	0.02

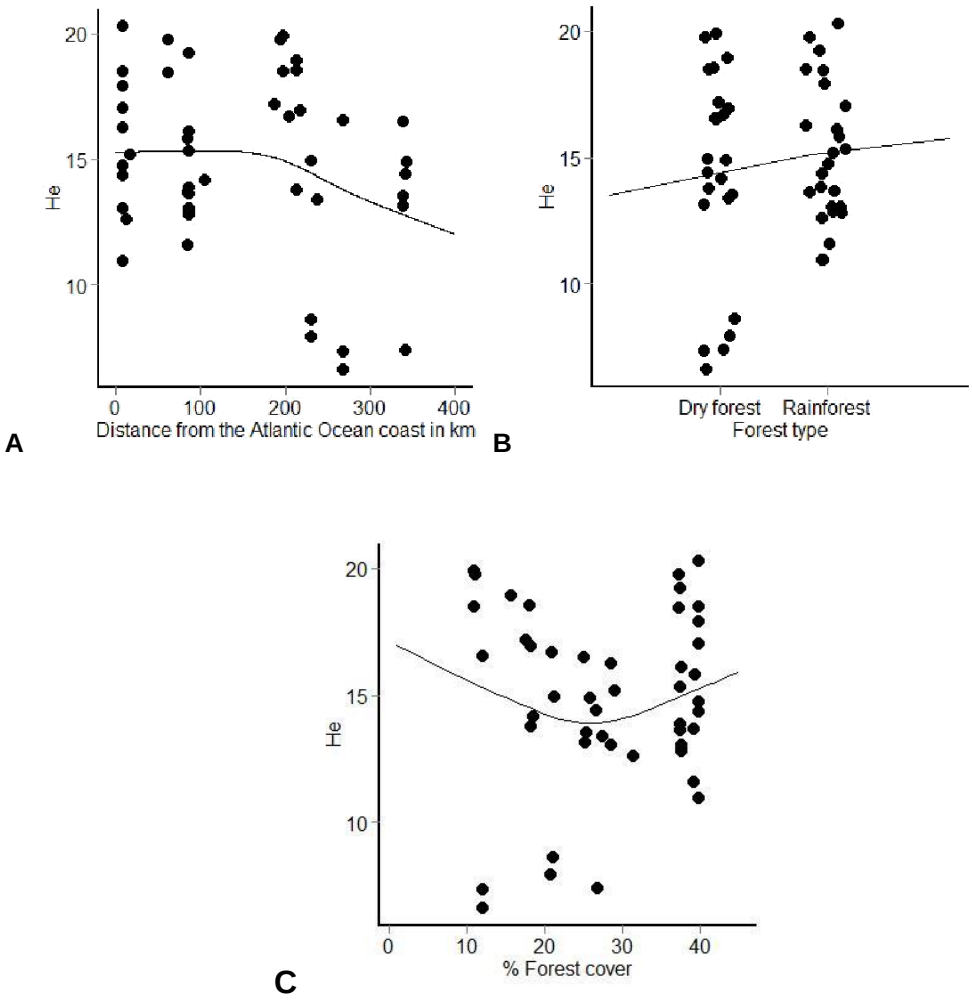

Fig. 3: Relationship between genetic diversity (H_e) and the predictive models selected by GAM analysis for populations of *Euterpe edulis* from 63 sites along Brazilian Atlantic Rainforest. **A** Effect of distance from Atlantic Ocean cost, **B** forest type, and **C** percentage of forest cover.

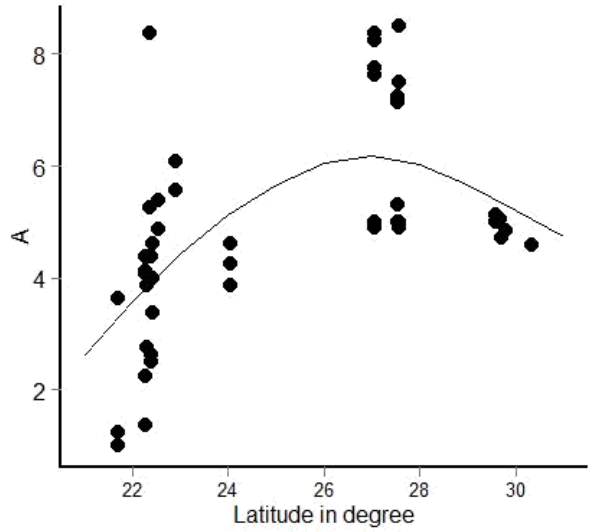

Fig. 4: Relationship between number of alleles (*A*) and the predictive model (latitude) selected by GAM analysis for populations of *Euterpe edulis* from 63 sites along Brazilian Atlantic Rainforest.

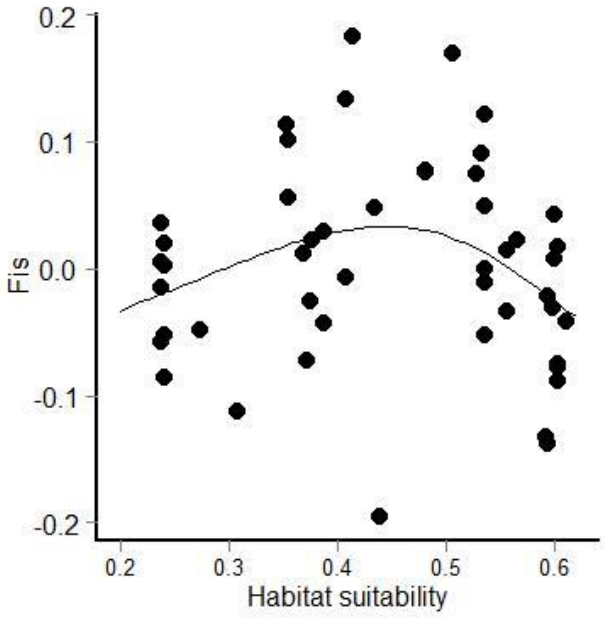

Fig. 5: Relationship between inbreeding coefficient (F_{IS}) and the predictive models (habitat suitability) selected by GAM analysis for population of *Euterpe edulis* from 63 sites along Brazilian Atlantic Rainforest.

Discussion

Despite the high fragmentation and habitat loss of Atlantic Rainforest, the genetic diversity and polymorphism are still very high in *E. edulis* populations. This may be due to the high effective population size, especially in populations of São Paulo (Galetti et al. 2013). However, we also observed that some populations showed high inbreeding, despite the predominantly outcrossed mating system (Gaiotto et al. 2003). This pattern was also observed for Neotropical trees, such as *Caryocar brasiliense* (Collevatti et al. 2001) and *Tabebuia aurea* (Braga & Collevatti 2011).

The Atlantic Rainforest is extremely heterogeneous due to its wide geographical range. An important East to West gradient in vegetation is observed, from a rainforest at the coast edges to a seasonally dry forest in the continent. In addition, the habitat loss and fragmentation of this biome is not random. The anthropic disturbance is higher in the continent, where flatlands favored the establishment of agriculture activities (Ribeiro et al. 2011). Therefore, we expect a decrease in genetic diversity from the Atlantic Ocean coast towards the continent. In fact, populations far from the coast have been suffering drastic size reduction due to agriculture expansion since ~1800 (Dean 1976). Additionally, *E. edulis* establishes only in wetter microhabitats in seasonally dry forests and riparian forests of the continent, which may strengthen isolation due to anthropogenic disturbance.

The latitude where number of alleles was higher (between 26° and 28° South) coincides with the most heterogeneous vegetation from Atlantic Rainforest biome (see Supplemental Information Fig. S5), which may favor population fine-scale sub-structuring, increasing genetic variability (Kawecki & Ebert 2004).

Our results showed that populations in habitats with higher suitability have lower F_{IS}. This may be due to higher effective population sizes in more suitable sites. However, sites with low values of habitat suitability also had low values of F_{IS}. We hypothesize that areas with low habitat suitability may have low support capacity for pollinators and seed dispersal populations which may force the movement among fragments seeking for food resources (Spear et al.

2010, e.g. White et al. 2002), increasing gene flow, and thus decreasing inbreeding.

Although forest amount could not explain alone the variation in genetic variability, distances from Atlantic Ocean coast and habitat suitability are related to the quantity of forest remaining. This controversial result may be the outcome of the differential response of genetic parameters to the severity of anthropic disturbance. In addition, the genetic effects of habitat fragmentation may be still undetectable using molecular markers because anthropogenic fragmentation is generally a recent event in evolutionary time, considering the life cycle of the species (Collevatti et al. 2001). Thus, the effect of disturbance may be detectable only after a certain threshold of disturbance is attainted (Collevatti et al. 2001). Moreover, genetic signatures resulting from historical bottlenecks may confound patterns of genetic diversity caused by the effects of recent fragmentation (see Ewers & Didham 2006 for a review).

Therefore, our results show that environmental heterogeneity (latitude), habitat suitability to establishment (habitat suitability) and human footprint (distance from Atlantic Ocean coast) have high influence on genetic variability in *E. edulis.* Thus, to conduct an efficient species conservation planning it is import to take into account not only humans impacts, such as habitat loss and fragmentation, but also habitat heterogeneity. Additionally, for a species conservation planning, we strongly recommend the incorporation of landscape genetics and large scale studies. In the foreseeable future, it is also important to investigate a local adaptation to different forest type.

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Supporting information

Table S1: Genetic parameters for populations of *Euterpe edulis* from 63 sites of Atlantic Rainforest. H_e, expected heterozigosity; F_{IS}, inbreeding coefficient; *A*, number of alleles per loci; Marker, molecular markers; Stage S, seedling, A, Adults.

Site	Coordinates		*He*	*Fis*	*A*	Marker	Stage	Publication
	Latitude	Longitude						
Caetetus1	-22.3835933	-49.6793777	0.82	0.15	11.0	Microsatellites	S	Carvalho et al. Carvalho et al. unpublished
Caetetus2	-22.3927875	-49.6899408	0.78	0.10	9.1	Microsatellites	S	Carvalho et al. Carvalho et al. unpublished
Caetetus3	-22.3779386	-49.6880782	0.79	0.20	11.9	Microsatellites	S	Carvalho et al. Carvalho et al. unpublished
Caetetus4	-22.3863716	-49.7273891	0.80	0.19	9.3	Microsatellites	S	Carvalho et al. Carvalho et al. unpublished
Candelária	-29.6691	-52.788304	0.24	-0.01	2.5	Isoenzyme	S	Martins-Conder et al. 2009
Caraá	-29.8	-50.3	0.26	-0.16	2.3	Isoenzyme	S	Martins-Conder et al.2009
Carlos Botelho1	-24.0617111	-47.993863	0.77	0.26	11.3	Microsatellites	S	Carvalho et al. unpublished
Carlos Botelho2	-24.0627184	-47.9886249	0.81	0.30	10.5	Microsatellites	S	Carvalho et al. unpublished
Carlos Botelho3	-24.059836	-47.9961286	0.79	0.25	10.9	Microsatellites	S	Carvalho et al. unpublished
Corumbataí2	-22.26770989	-47.67068599	0.74	0.14	8.9	Microsatellites	S	Carvalho et al. unpublished
Corumbataí3	-22.26953832	-47.64513829	0.80	0.22	10.8	Microsatellites	S	Carvalho et al. unpublished
Corumbataí4	-22.28048022	-47.66162943	0.73	0.18	8.0	Microsatellites	S	Carvalho et al. unpublished
Desengano	-21.970085	-41.99924	0.14	-	-	AFLP	A	Cardoso et al. 2000
Dinamérica1	-22.2932761	-49.6274955	0.79	0.20	10.5	Microsatellites	S	Carvalho et al. unpublished
Dinamérica2	-22.2893228	-49.626896	0.72	0.13	9.4	Microsatellites	S	Carvalho et al. unpublished
Guaraqueçaba	-25.287364	-48.317037	0.16	-	-	AFLP	A	Cardoso et al. 2000
Ibirama	-27.053842	-49.543448	0.40	0.07	3.1	Aloenzyme	A	Conte et al. 2008
Ibirama	-27.053842	-49.543448	0.44	0.10	3.0	Aloenzyme	S	Conte et al. 2008
Ibirama	-27.053842	-49.543448	0.79	0.12	14.9	Microsatellites	A	Conte et al. 2008
Ibirama	-27.053842	-49.543448	0.79	0.16	14.3	Microsatellites	S	Conte et al. 2008
Ibirama 2	-27.052843	-49.539762	0.41	0.08	3.0	Aloenzyme	A	Conte et al. 2008
Ibirama 2	-27.052843	-49.539762	0.38	0.07	3.0	Aloenzyme	S	Conte et al. 2008
Ibirama 2	-27.052843	-49.539762	0.78	0.09	15.0	Microsatellites	A	Conte et al. 2008
Ibirama 2	-27.052843	-49.539762	0.78	0.12	14.4	Microsatellites	S	Conte et al. 2008
Ilha Grande	-23.152084	-44.228944	0.14	-	-	AFLP	A	Cardoso et al. 2000
Ipeúna1	-22.41412221	-47.66420636	0.79	0.15	10.0	Microsatellites	S	Carvalho et al. unpublished
Ipeúna2	-22.42216221	-47.66155173	0.84	0.04	11.3	Microsatellites	S	Carvalho et al. unpublished
Ipeúna3	-22.41561351	-47.67273252	0.82	0.04	10.6	Microsatellites	S	Carvalho et al. unpublished
Iracemápolis1	-22.5575219	-47.58113449	0.84	0.14	12.0	Microsatellites	S	Carvalho et al. unpublished
Iracemápolis2	-22.54200465	-47.56554248	0.85	0.20	11.5	Microsatellites	S	Carvalho et al. unpublished
Iracemápolis3	-22.55487833	-47.58175886	0.85	0.19	11.5	Microsatellites	S	Carvalho et al. unpublished
Itatiaia	-22.495735	-44.560951	0.14	-	-	AFLP	A	Cardoso et al. 2000
Linhares	-19.389282	-40.064515	0.09	-	-	AFLP	A	Cardoso et al. 2000
Magé	-22.656704	-43.039803	0.13	-	-	AFLP	A	Cardoso et al. 2000
Mariana Pimentel	-30.353219	-51.584054	0.25	-0.08	2.0	Isoenzyme	S	Martins-Conder et al.2009

Maricá	-22.919092	-42.818285	0.81	0.17	12.2	Microsatellites	A	Seone et al. 2005
Maricá	-22.919092	-42.818285	0.78	0.31	12.7	Microsatellites	S	Seone et al. 2005
Nova Friburgo	-22.287136	-42.533698	0.84	0.25	10.7	Microsatellites	A	Seone et al. 2005
Nova Friburgo	-22.287136	-42.533698	0.85	0.25	11.0	Microsatellites	S	Seone et al. 2005
Pindamonhagaba	-22.923593	-45.45978	0.14	-	-	AFLP	A	Cardoso et al. 2000
Santa Cruz do Sul	-29.723992	-52.436044	0.27	0.22	2.1	Isoenzyme	S	Martins-Conder et al.2009
Santa Teresa	-19.931464	-40.595243	0.12	-	-	AFLP	A	Cardoso et al.2000
São Pedro de Alcântara	-27.568787	-48.805727	0.26	0.07	2.4	Aloenzyme	S	Conte et al. 2003
São Pedro de Alcântara	-27.568787	-48.805727	0.28	0.01	2.6	Aloenzyme	A	Conte et al. 2003
São Pedro de Alcântara	-27.568787	-48.805727	0.43	0.11	3.1	Aloenzyme	S	Conte et al. 2008
São Pedro de Alcântara	-27.568787	-48.805727	0.43	0.06	3.0	Aloenzyme	A	Conte et al. 2008
São Pedro de Alcântara	-27.568787	-48.805727	0.80	0.16	14.1	Microsatellites	S	Conte et al. 2008
São Pedro de Alcântara	-27.568787	-48.805727	0.79	0.12	15.1	Microsatellites	A	Conte et al. 2008
São Pedro de Alcântara 2	-27.554147	-48.796604	0.45	-0.01	3.4	Aloenzyme	S	Conte et al. 2008
São Pedro de Alcântara 2	-27.554147	-48.796604	0.42	0.08	3.1	Aloenzyme	A	Conte et al. 2008
São Pedro de Alcântara 2	-27.554147	-48.796604	0.76	0.10	13.9	Microsatellites	S	Conte et al. 2008
São Pedro de Alcântara 2	-27.554147	-48.796604	0.76	0.09	13.8	Microsatellites	A	Conte et al. 2008
Serra Grande	-12.733333	-39.616667	0.09	-	-	AFLP	A	Cardoso et al. 2000
Tambaú1	-21.69444194	-47.3287522	0.72	0.23	7.6	Microsatellites	S	Carvalho et al. unpublished
Tambaú2	-21.69685777	-47.32246351	0.72	0.28	7.9	Microsatellites	S	Carvalho et al. unpublished
Tambaú3	-21.69213206	-47.33760777	0.82	0.29	10.3	Microsatellites	S	Carvalho et al. unpublished
Terra de Areia	-29.594215	-50.075947	0.23	0.20	2.4	Isoenzyme	S	Martins-Conder et al.2009
Tinguá	-22.6	-43.433331	0.11	-	-	AFLP	A	Cardoso et al. 2000
Torres	-29.339114	-49.727032	0.20	-0.01	2.2	Isoenzyme	S	Martins-Conder et al.2009
Uma	-15.269563	-39.069421	0.11	-	-	AFLP	A	Cardoso et al. 2000
Venâncio Aires	-29.606038	-52.194403	0.28	0.08	2.5	Isoenzyme	S	Martins-Conder et al.2009
São José	-22.359039	-47.477008	0.84	0.13	15.0	Microsatellites	S	Carvalho et al. unpublished

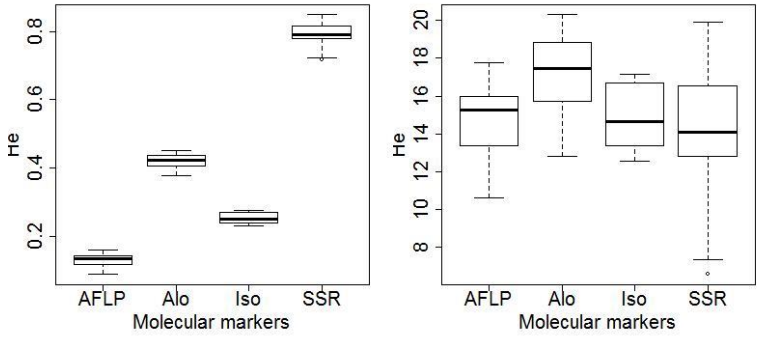

Fig. S1: The effect of molecular markers on genetic diversity (H_e). A: median *He,* among sites*,* for each molecular marker, B: median *He* among sites, for each molecular marker, taking out the marker effect. Molecular markers are: SSR= Microsatellites, Iso= Isoenzyme, Alo= Aloenzyme and AFLP= Amplified Fragment Length Polymorphism). The center horizontal line is the median of the sample. The top of the box above the median shows the 75th percentile and the

bottom of the box bellow the median shows the 25th percentile. The whiskers show the maximum and minimum value of the sample.

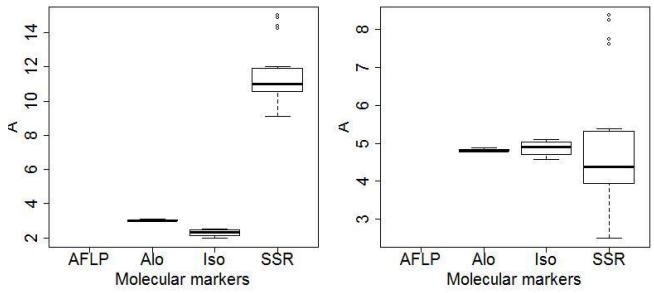

Fig. S2: The effect of molecular markers on number of alleles (*A*). A: median *A,* among sites*,* for each molecular marker, B: median *A* among sites, for each molecular marker, taking out the marker effect. Molecular markers are: SSR= Microsatellites, Iso= Isoenzyme, Alo= Aloenzyme and AFLP= Amplified Fragment Length Polymorphism). The center horizontal line is the median of the sample. The top of the box above the median shows the 75th percentile and the bottom of the box bellow the median shows the 25th percentile. The whiskers show the maximum and minimum value of the sample.

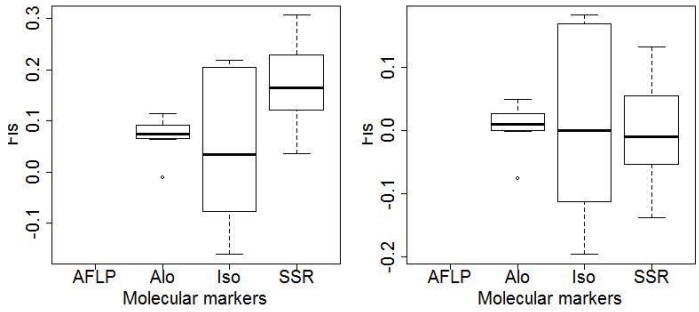

Fig. S3: The effect of molecular markers on inbreeding coefficient (F_{IS}). A: median F_{IS}*,* among sites*,* for each molecular marker, B: median F_{IS} among sites, for each molecular marker, taking out the marker effect. Molecular markers are: SSR= Microsatellites, Iso= Isoenzyme, Alo= Aloenzyme and AFLP= Amplified Fragment Length Polymorphism). The center horizontal line is the median of the sample. The top of the box above the median shows the 75th percentile and the bottom of the box bellow the median shows the 25th percentile. The whiskers show the maximum and minimum value of the sample.

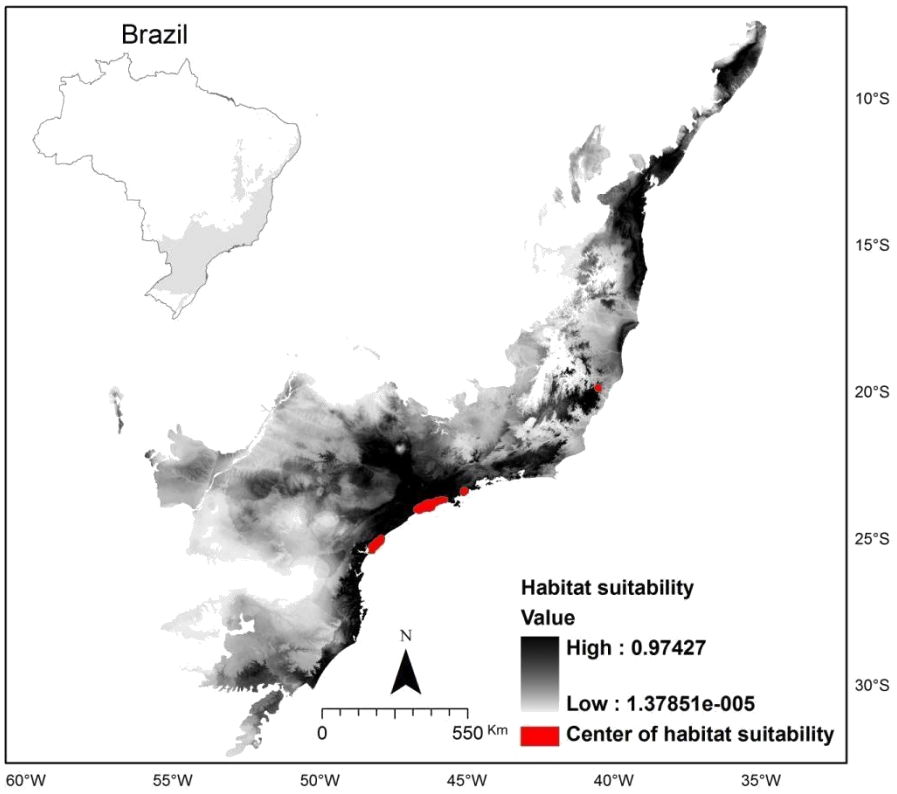

Fig. S4: Map of mean habitat suitability model for *Euterpe edulis* using Maxent method and five bioclimatic variables from the WorldClim, altitude and forest cover.

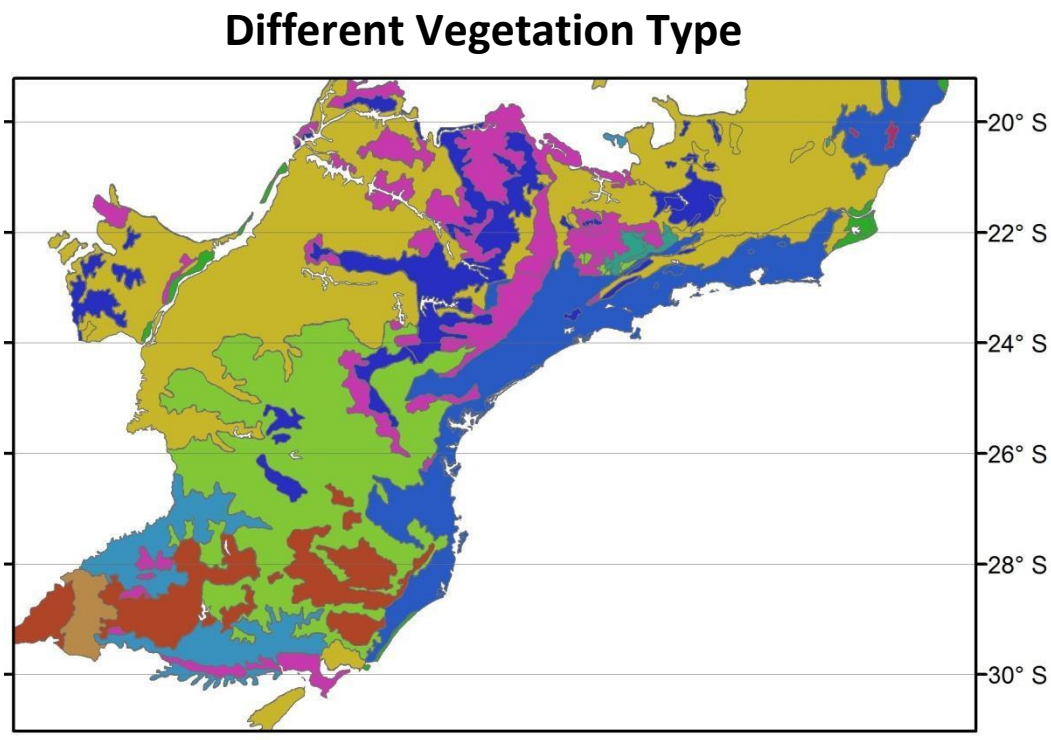

Fig. S5: Map of vegetation type of Atlantic Rainforest adapted from Ribeiro et al. 2011.

Table S2: Correlation values among explanatory metrics (correlation/p) of 63 study sites with genetic information for *Euterpe edulis* across the Brazilian Atlantic Rainforest biome in Brazil.

	% Forest cover	Defaunation	Functional connectivity	Distance from the Atlantic Ocean coast	Setting data	Forest type	Northness	Eastness	Declivity	Latitude	Drainage density	Habitat suitability	Distance from the locality with highest habitat suitability
% Forest cover	1.00	0.57	0.00	0.21	0.01	0.14	0.12	0.84	0.09	0.03	0.01	0.67	0.41
Defaunation	-0.09	1.00	0.52	0.18	0.20	0.15	0.55	0.54	0.85	0.39	0.01	0.02	0.70
Functional connectivity	0.90	0.10	1.00	0.70	0.00	0.72	0.34	0.44	0.18	0.00	0.02	0.61	0.32
Distance from the Atlantic Ocean coast	0.19	0.20	0.06	1.00	0.39	0.00	0.15	0.41	0.21	0.01	0.58	0.00	0.66
Setting data	0.40	-0.20	-0.57	0.13	1.00	0.24	0.63	0.01	0.44	0.00	0.33	0.35	0.62
Forest type	0.23	0.22	0.06	-0.77	0.18	1.00	0.97	0.21	0.04	0.00	0.87	0.00	0.02
Northness	0.24	0.09	-0.15	-0.22	0.07	-0.01	1.00	0.00	0.05	0.44	0.68	0.10	0.82
Eastness	-0.03	-0.10	-0.12	0.13	-0.37	0.19	0.79	1.00	0.29	0.00	0.78	0.04	0.13
Declivity	0.26	0.03	-0.21	-0.19	-0.12	0.31	-0.29	-0.16	1.00	0.06	0.69	0.34	0.00
Latitude	-0.32	-0.13	0.61	-0.42	0.57	-0.47	-0.12	0.44	0.29	1.00	0.57	0.01	0.91
Drainage density	0.40	0.40	-0.35	0.09	0.15	0.03	-0.06	0.04	-0.06	0.09	1.00	0.01	0.35
Habitat suitability	0.07	-0.36	0.08	-0.43	-0.14	-0.49	-0.25	0.32	0.15	-0.38	0.38	1.00	0.04
Distance from the locality with highest habitat suitability	0.13	0.06	-0.15	0.07	0.08	-0.36	0.03	0.23	0.46	0.02	0.14	-0.30	1.00

CAPÍTULO 2

MATRIX RESISTANCE AND HABITAT LOSS DETERMINES PATTERNS OF GENETIC DIFFERENTIATION IN A RAINFOREST PALM SPECIES

Title: Matrix resistance and habitat loss determines patterns of genetic differentiation in a Rainforest palm species

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Abstract

Human activities have transformed tropical forest around the Planet into biologically impoverished patches. Habitat loss and fragmentation are pointed out as the mainly anthropogenic factors in species richness and abundance and genetic variability decreasing. Therefore, we evaluated here if habitat fragmentation and habitat loss affect genetic variability and differentiation in *Euterpe edulis,* a palm that is widely distributed in Atlantic Rainforest. We also tested the contribution of geographic distance to explain the genetic structure. Seven landscapes were analyzed in Sao Paulo State, Southeast Brazil, summing up 22 sites and the genetic variability and differentiation were accessed using eight microsatellites loci. We measured the relative contribution of percentage of forest cover, site isolation, functional connectivity and matrix resistance on genetic variability and differentiation using multiple competing hypothesis and model comparison based on AIC (Akaike's Information Criteria). None of the models explained the variation observed in genetic diversity (H_e) and allelic richness. Variation in inbreeding coefficient (F_{IS}) among sites was best explained by matrix resistance cost and site isolation. Matrix resistance cost also explained variation observed in pairwise F_{ST} among sites, together with percentage of forest cover. Therefore, our study showed that habitat loss and fragmentation are less important for *E. edulis* genetic variability and differentiation, or harder to detect than the effects of landscape features stressing the importance of including these landscape feature variables when seeking to understand the key ecological processes associated to dispersal.

Introduction

Neotropical forests have been severely impacted by habitat loss and fragmentation, resulting in biologically impoverished patches (Laurance et al. 2004, Nogueira et al. 2007). These factors affect species richness and abundance, as well as several key ecological processes (Fahrig 2003) such as seed dispersal (e.g. Uriarte et al. 2011), pollination (e.g. Gonzalez-Varo et al. 2009, but see Breitbach et al. 2012) and fauna movement (Eycott et al. 2012); and consequently, genetic variability (e.g. Moreira et al. 2009; Collier et al. 2010; see DiBattista 2008 for a review).

The reduction in species richness and abundance can be associated with the amount of available habitat and the reduction in patch size (Fahrig 2003, Prugh et al. 2008). For example, this relationship was observed for non-volant small mammals, large canopy birds, frugivorous and omnivorous birds (Pardini et al. 2005, Uezu et al. 2005, Martensen et al. 2008, 2012). Habitat loss and fragmentation are also pointed out as the main anthropogenic factors that reduce genetic variability (Lowe et al. 2005, Aguilar et al. 2008, DiBattista 2008) as an outcome of drastic reduction in population size (e.g. Frankham et al. 1999, Andersen et al. 2004). In small populations, the probability of mating between closely related individuals increase, and together with random genetic drift may also lead to a substantial reduction in genetic variability (e. g. Breed et al. 2012). The loss of genetic variability may reduce individual fitness (Reed & Frankham 2003, Bijlsma & Loeschcke 2012), and also species evolutionary capacity to cope with environmental changes (Hoffmann & Willi 2008, Taubmann et al. 2011).

The mobility and dispersal of animals and plants are also affected by habitat loss and fragmentation (Diffendorfer et al. 1995, Awade & Metzger 2008, Puttker et al. 2011). Movements of organisms across fragmented landscapes depend on life history traits and landscape characteristics, such as matrix quality (Antongiovanni & Metzger 2005, Umetsu & Pardini 2007, Umetsu et al. 2008) and distance among forested areas (Boscolo & Metzger 2011). The isolation of populations, which is indentified by the resistance of the intervenient matrix, may limit the dispersal among populations, reducing gene flow and population connectivity (e.g. Coulon et al. 2004, Johansson et al. 2007, Lange

et al. 2012). This may cause disruption on the migration-drift equilibrium, because alleles lost by random genetic drift may not be replenished by gene migration (Hamrick 2004).

Although population genetic theory predicts habitat loss and fragmentation effects on population genetic structure (Young et al. 1996), diverse empirical studies are not supporting this theory in plants (e.g. Collevatti et al. 2001, Bacles et al. 2005, Winkler et al. 2011, Aparicio et al. 2012). Different factors can influence the non-detection of fragmentation effects on plant genetic structure, among them, life history traits and the time-lag effect (Kramer et al. 2008). For example, insect-pollinated trees and shrubs are more likely to lose genetic variability due to fragmentation than bird-pollinated because of differences in mobility between insects and birds (e. g. Kramer et al. 2011, see Vranckx et al. 2011 for review). Alike, self-compatibles plants may be less affected by habitat loss and fragmentation than obligate outcrossing plants (Honnay & Jacquemyn 2007, Aguilar et al. 2008).

The relationships of genetic variability and differentiation with landscape structure are highly complex due to the diverse and potentially interacting process, such as habitat loss, population dynamics, dispersal strategy, matrix resistance to dispersal and mating system (Wagner & Fortin 2012). For example, the genetic signatures resulting from demographical history, such as bottleneck events, may confound patterns of genetic diversity caused by the effects of recent fragmentation (see Ewers & Didham 2006 for a review on fragmentation of confounding factors). Also, genetic effects of habitat fragmentation may be still undetectable because of long life cycles (Collevatti et al. 2001, Collevatti et al. 2013). Thus, it is important to disentangle proximate and historical factors when evaluating fragmentation effects on genetic variability.

Although many studies show the effect of habitat loss and fragmentation on genetic variability, most of them focus on a given landscape (e.g. Kettle et al. 2007, Collier et al. 2010) and are not designed to compare different landscapes (i.e. few km^2 of extent; Bruggeman et al. 2010, Bacles & Jump 2011). Moreover, most studies do not include explicitly test of the influence of landscape features on genetic differentiation (e.g. Chambers & Garant 2010 and see Storfer et al. 2010 for review). Thus, a more in-depth analysis, evaluating the effect of

different landscape features on genetic variability and gene flow is helpful to better understand the contribution of the different landscape components in genetic variability (see Storfer et al. 2007 for a review).

The Atlantic Rainforest biome was one of the largest tropical rainforests of the Americas (Mittermeier et al. 2005). However it was reduced to 11.7% of its original 150 millions ha (Ribeiro et al. 2009), resulting in continental islands of wild habitat surrounded by crops, pastures and urban matrix, jeopardising species viability. This ecosystem is one of the 25' biodiversity hotspots because of its high biodiversity and severe anthropic disturbance (Mittermeier et al. 2005). Thus, it is a good model system to quantify the effects of habitat loss and fragmentation on genetic variability and gene flow. *Euterpe edulis* (Arecaceae) is an endangered palm species, once one of the dominant palms of Atlantic Forest (Henderson et al. 1995). Its edible meristem (heart of palm or "palmito juçara") is source of raw material for small and middle size industries, based mainly on the illegal extrativism, which contributes to its threaten (Galetti & Fernandez 1998). *Euterpe edulis* is a self-compatible monoecious species but with predominant allogamous reproduction and pollination performed mainly by small-sized bees, such as *Trigona spinipes* (Reis et al. 1993). A great variety of bird species, from large frugivorous (e.g. *Procnias* spp., *Penelope* spp., *Ramphastos* spp.) to small birds, such as thrushes (*Turdus* spp.) may disperse the seeds (Galetti et al. 1999, 2013).

Herein, we evaluated the relative contribution of habitat loss, fragmentation and matrix resistance on genetic variability and differentiation of *E. edulis.* For this, we analyzed the effect of different landscape structure, such as percentage of forest cover, patch isolation, functional connectivity, and matrix resistance on population genetic diversity, inbreeding, allelic richness and genetic differentiation among *E. edulis* populations. Concomitantly, we also tested the contribution of geographic distance in the variability of genetic differentiation among patches.

Material and Methods

Landscape and sites selection

The study was carried out in landscapes of Atlantic Rainforest within São Paulo state, Southeast Brazil (Fig.1). The Atlantic Rainforest fragmentation in São Paulo is very ancient (since ~1800, Dean 1976) and currently, besides the middle and large cities, the forest remnants are surrounded by many different matrix, such as sugar cane, cattle pasture, planted forestry (mainly *Eucalyptus* spp. and *Pinus* spp.) and coffee culture, which allow the analysis of matrix resistance effects on genetic diversity of focal species (Ribeiro et al. 2011).

We sampled 22 sites within seven landscapes distributed in a gradient of forest cover from 5% to 75% (Fig. 1 and Fig. 2). The choice of this gradient in forest cover and landscape size were based on the observed threshold for severe species loss (10-30%, Radford et al. 2005, Pardini et al. 2010; and 30-50%, Martensen et al. 2012). Each landscape had 2km of radius around a midpoint. We chose this radius because some frugivorous species taxonomically related with the seed disperses of our focal plant species present dispersal distance lower than 600m (Jordano et al. 2007, Holbrook 2011). Also, species occurrence within São Paulo state is best explained by landscape features at this spatial scale (Boscolo & Metzger 2009, Lyra-Jorge et al. 2010). Besides the forest cover gradient, we also selected landscape with at least two forest patches or sites with *E. edulis* (see Supporting Information Table S1 for details on the 22 sites within the seven landscapes).

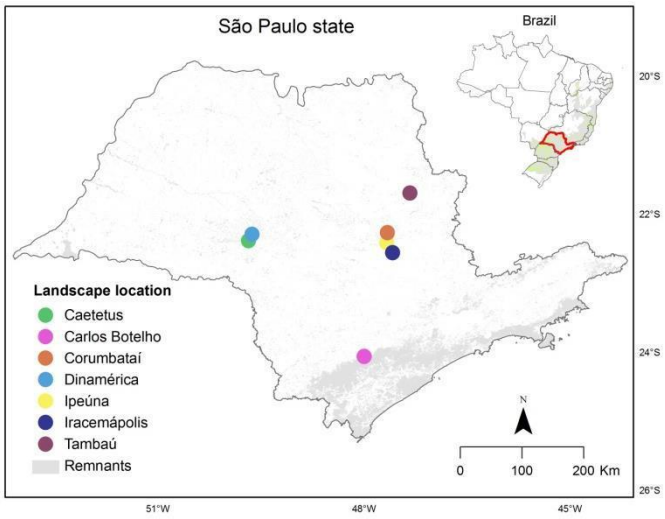


Fig. 1: The seven selected landscape with Atlantic Rainforest remnants and presence of *Euterpe edulis*, in São Paulo state, Southeast Brazil. The Brazil map shows the original distribution of Atlantic Rainforest.

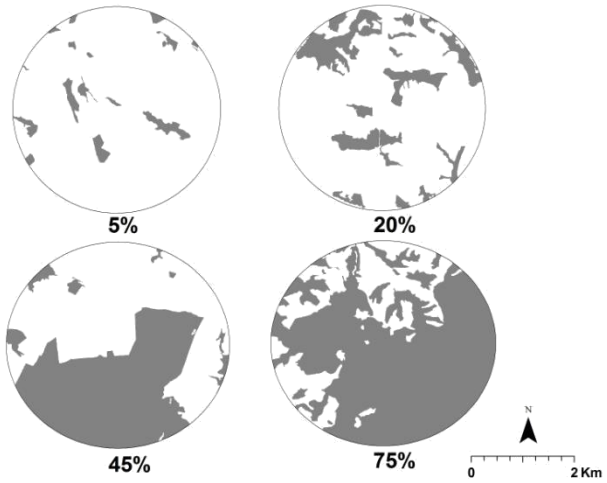


Fig. 2: Examples of sampled landscapes (2km of radius) with different percentages of Atlantic Rainforest cover (5%, 20%, 45% and 75%) and presence of *Euterpe edulis*, in São Paulo state, Southeast Brazil.

Explanatory metrics

We mapped all selected landscapes using visual digitalization and classification at the scale of 1:5,000. High resolution 1x1m images were available on Google Earth (http://earth.google.com). QGIS (www.qgis.org) software was used in this step because it allows the access to the images on the fly by using OpenLayer plugin (OpenLayer, 2012). The landscapes were than classified in 13 different classes: advanced forest, intermediate forest succession, pioneer forest, initial regeneration, *Eucalyptus sp.*, sugar cane, coffee plantation, swamp area, swamp area with isolated trees, pasture, pasture with isolated trees, mining areas, rural building (see Supporting Information Fig. S1 for an example of mapping).

The analyses were carried out in two scales: landscape-site scale and pairwise scale (Fig. 3). At the landscape-site scale we calculated: (1) percentage of forest cover around the focal site, (2) functional connectivity, (3) matrix resistance and (4) site isolation. At the pairwise scale we estimated: (1) matrix resistance, (2) geographic distance and (3) percentage of forest cover (see Supporting Information S2 for details on the explanatory metrics calculation).

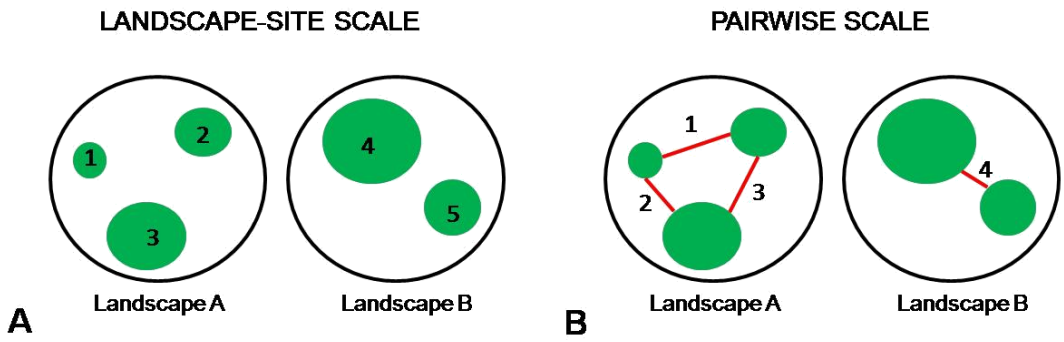


Fig. 3: Scale analysis for *Euterpe edulis* in Atlantic Rainforest remnants in São Paulo state, Southeast Brazil. **A**. Landscape-site scale and **B.** Pairwise scale. Green circles represent sampling sites and black circles the landscapes.

Percentage of forest cover measures the quantity of native forest around the focal site in landscape-site scale analysis, and within each landscape with 2 km-radius in pairwise scale. Functional connectivity measures how easy is the biological flow in a specific landscape (Taylor et al. 1993) taking into account the intrinsic capacity of individual dispersal between sites (Uezu et al. 2005, Awade & Metzger 2008). In this case, we use *Turdus* sp. distance dispersal (Jordano et al. 2007, Supporting Information S2). To obtain matrix resistance we used the analysis implemented in the software Loracs (Pinto et al. 2012) based on the theory of graphs (Urban & Keitt 2001). The software applies search algorithms (Dijkstra 1959) to identify optimum routes between two points. Using a resistance surface file, we calculated the mean cost and the mean length (the ratio of distance to move among sites and the cost) to move among sites (see Supporting Information S2). Fragment isolation was measured calculating the mean geographic distance from border to border among all sites within the landscapes. Geographic distance was calculated by Euclidean distance between two sites. Following the calculation of all landscape metrics, we analyzed the correlation among all variables (Supporting Information Table S4 and Table S5).

Seedling sampling and genetic analyses

In each site we sampled ~ 30 seedlings (in a total of 636 individuals, see Supporting Information Table S1). We used seedlings to minimize the effect of

time-lag on genetic responses, because old individuals may respond to previous landscape (Metzger et al. 2009). To avoid or minimize effects of spatial autocorrelation, seedlings were sampled at 10 meters of distance (Carvalho et al. 2010).

For genetic data analysis, all individuals were genotyped using eight microsatellite loci, following Gaiotto et al. (2001). To describe the genetic variability, we estimated the genetic diversity (H_e - expected heterozigosity following Nei 1978), the allelic richness (*AR*, Mousadik & Petit 1996) and inbreeding coefficient (F_{IS}). We also estimated genetic differentiation among all pairs of sites using Wright's F_{ST} (Wright 1951), obtained from an analysis of variance of allele frequencies (Weir & Cockerham 1984). All analyses were carried out using the software FSTAT 2.9.3.2 (Goudet 2002).

Linking genetic and landscape data

We defined a set of *a priori* models (Fig. 4) to explain the genetic response variables. First, we tested three different methods of fit the data: Generalized Linear Model (GLM, R Core Team 2012), Generalized Addition Models (GAM – "gam" R package, Hastie 2012) and Maximum Likelihood Estimation (MLE – "bbmle" R package, Bolker 2012). We choose the best-fitted model for each hypothesis using Akaike Information Criterion (AIC – see below). For all genetic variables, but F_{ST}, the best model was MLE. For F_{ST} we used GAM to analyze the mean cost using Loracs and GLM to analyze mean length using Loracs and geographical distance.

As the influence of landscape in genetic variables tends to be complex and depend of the interaction of diverse factors (Boscolo & Metzger 2011), we used model selection with multiple competing hypotheses approach (Burnhan & Anderson 2002) following our predictions (Fig. 4). We calculated AIC corrected for small samples and AICci (where *i* represents each model). Models with AICc < 2 are equally plausible to explain the observed pattern (Zuur et al. 2009). We also obtained Akaike's weight of evidence (wAICc) using this measure as the relative contribution of model *i* to explain the observed pattern, given a set of compete models (Burnhan & Anderson 2002). The AIC analyses were performed with R package "bbmle" (Bolker 2012).

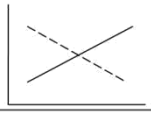
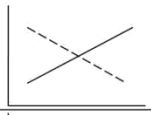
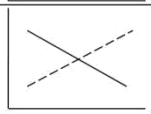
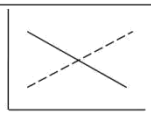
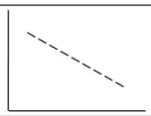
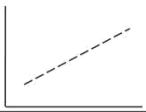
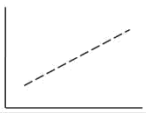
Scale of analysis	Genetic parameters	Explanatory metrics	Hypothesis
Landscape scale	H_e F_{IS} AR	% Forest cover around the focal site	
	H_e F_{IS} AR	Functional connectivity	
	H_e F_{IS} AR	Matrix resistance	
	H_e F_{IS} AR	Site isolation	
Pairwise scale	F_{ST}	% Forest cover	
	F_{ST}	Matrix resistance	
	F_{ST}	Geographic distance	

Fig. 4: Genetic predictions in relation to each landscape variable. Column of genetic parameters corresponds to y axes on graph hypothesis and column of explanatory metrics corresponds to x axes. In landscape-site scale, continuous lines represent genetic diversity (H_e) and allelic richness (AR), and dotted lines represent inbreeding coefficient (F_{IS}). In pairwise scale, dotted lines represent pairwise genetic differentiation (F_{ST}).

Results

Genetic variability and differentiation

All pairs of microsatellite loci were in linkage equilibrium (all $p > 0.05$) and all loci presented high genetic variability (Supporting Information Table S6). Although the observed heterozygosity deviate from the expected for Hardy-Weinberg equilibrium for all loci (all $p < 0.001$), the high combined paternity exclusion (0.99999) and low probability of identity (2.03x10-15) showed that the eight loci are suitable for individual discrimination.

Genetic diversity (H_e) and allelic richness (AR) was high in all populations, ranging from 0.716 to 0.864 and from 6.2 to 9.5, respectively (Table 1). However, the inbreeding coefficient (F_{IS}) was high and significant for all populations.

Populations are significantly differentiated (F_{ST} = 0.106, SE = 0.010, p < 0.001) and the analysis also showed that inbreeding is an important factor in population differentiation (F_{IS} = 0.186, SE = 0.029, p < 0.001). Pairwise F_{ST} ranged from 0.002 to 0.20 (Supporting Information Table S7).

Table 1. Genetic variability in 22 sites of *Euterpe edulis* in Atlantic Rainforest remnants in São Paulo state, Southeast Brazil. N – number of individuals sampled; H_e - expected heterozigosity; H_o - observed heterozigosity; F_{IS}, inbreeding coefficient (* significant, p < 0.001); AR - allelic richness. For sites details see Supporting Information Table S1.

Landscape	Sites	N	H_e	H_o	F_{IS}	AR
Caetetus	CA1	30	0.815	0.695	0.148*	9.0
	CA2	30	0.781	0.702	0.101*	7.5
	CA3	30	0.786	0.631	0.197*	9.2
	CA4	31	0.799	0.651	0.186*	7.4
Carlos Botelho	CB1	30	0.766	0.564	0.264*	8.8
	CB2	30	0.808	0.571	0.295*	8.6
	CB3	30	0.797	0.591	0.248*	8.6
Corumbatai	CO1	14	0.864	0.661	0.235*	9.0
	CO2	28	0.736	0.631	0.143*	6.9
	CO3	28	0.799	0.627	0.216*	8.3
	CO4	30	0.729	0.597	0.182*	6.3
Dinamérica	DI1	30	0.794	0.633	0.203*	8.6
	DI2	30	0.724	0.629	0.131*	7.5
Ipeúna	IP1	26	0.788	0.668	0.152*	8.4
	IP2	29	0.836	0.806	0.036	8.9
	IP3	27	0.819	0.786	0.041	8.7
Iracemápolis	IR1	30	0.835	0.717	0.141*	9.5
	IR2	30	0.848	0.681	0.196*	9.3
	IR3	31	0.849	0.689	0.189*	9.3
Tambaú	TA1	31	0.716	0.551	0.230*	6.2
	TA2	31	0.724	0.524	0.275*	6.4
	TA3	30	0.816	0.581	0.288*	8.3

Linking genetic and landscape data

None of the models explained the variation observed in genetic diversity (H_e) and allelic richness (*AR*) (Table 5). Inbreeding coefficient (F_{IS}) was best explained by matrix resistance cost and site isolation (Table 5). However, the relationship between these variables and F_{IS} was not clear, but F_{IS} tended to be lower in populations at landscapes with high matrix resistance cost and isolation among sites (Fig. 5A, 5B). Matrix resistance cost also explained the variation observed in pairwise F_{ST} among sites (Table 6) and together with percentage of forest cover explained 89% of the variation observed in pairwise F_{ST} (Table 6). Populations at landscapes with higher matrix resistance cost present lower levels of differentiation, although the same pattern was observed in landscapes with very low matrix resistance cost (Fig. 6A). Pairwise differentiation was negatively related with percentage of forest cover (Fig. 6B).

Table 5: Model selection for H_e (expected heterozygosity), F_{IS} (inbreeding coefficient) and *AR* (allelic richness) in 22 sites of *Euterpe edulis* in Atlantic Rainforest remnants in São Paulo state, Southeast Brazil. K= number of parameters estimated for each model.

Models	H_e			F_{IS}			*AR*		
	K	ΔAICc	wAICc	K	ΔAICc	wAICc	K	ΔAICc	wAICc
% forest cover around the focal site	3	0.7	0.14	3	4.7	0.04	3	1.3	0.14
Functional connectivity	3	0.6	0.15	3	4.5	0.04	3	0.4	0.22
Matrix resistance cost	3	0.3	0.17	3	0.0	0.42	3	1.8	0.11
Matrix resistance length	3	0.0	0.20	3	2.0	0.15	3	2.0	0.10
Site isolation	3	0.7	0.14	3	0.7	0.30	3	0.0	0.27
Null model	3	0.2	0.18	3	5.0	0.03	3	1.1	0.15

Table 6: Model selection for genetic differentiation pattern, measured by pairwise $F_{ST,}$ among 22 sites of *Euterpe edulis* in Atlantic Rainforest remnants in São Paulo state, Southeast Brazil. K= numbers of parameters estimated for each model.

Models	K	ΔAICc	wAICc	Cumulative wAICc
Matrix resistance cost+ % forest cover	4	0.0	0.61	0.89
Matrix resistance cost	3	1.6	0.28	
% forest cover	3	3.9	0.09	0.11
Matrix resistance length	3	7.9	0.01	
Geographic distance	3	8.9	>0.01	
Null model	3	9.2	>0.01	

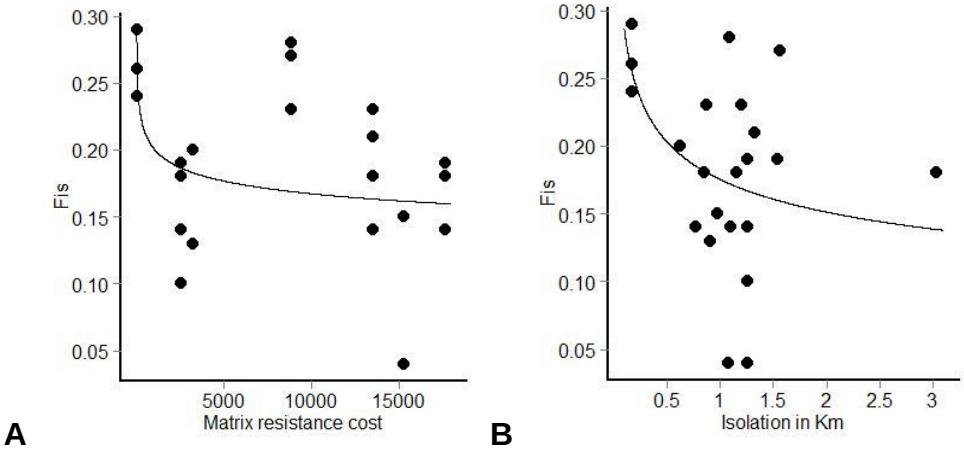


Fig. 5: Relationship of pairwise F_{IS} and matrix resistance cost and site isolation for 22 sites of *Euterpe edulis* in Atlantic Rainforest remnants of São Paulo state, Southeast Brazil.

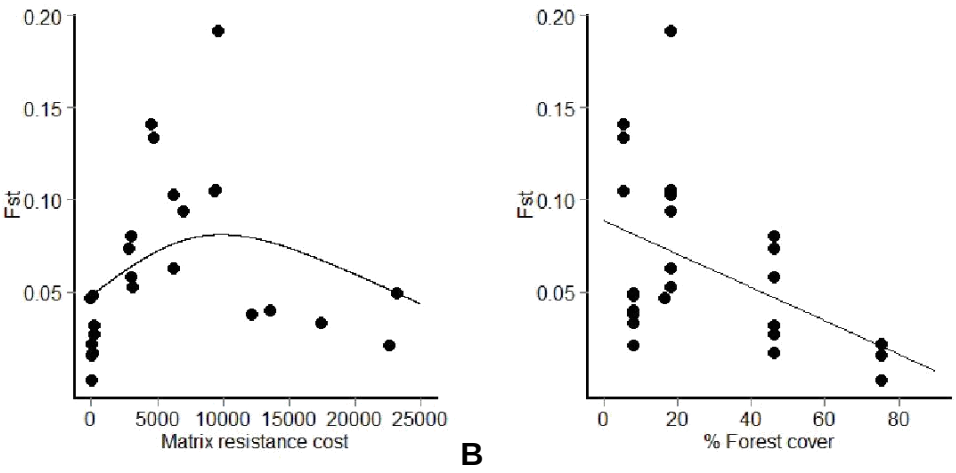


Fig. 6: Relationship of pairwise F_{ST} and matrix resistance cost and percentage of forest cover for 22 sites of *Euterpe edulis* in Atlantic Rainforest remnants of São Paulo state, Southeast Brazil.

Discussion

Despite the high anthropogenic disturbance and fragmentation of the studied landscapes, our results showed high level of genetic diversity and polymorphism for *E. edulis* in all populations and no relationship with landscape features. The high genetic diversity was also reported for *E. edulis* in other regions of Atlantic Rainforest (e.g. Gaiotto et al. 2003, Seoane et al. 2005, Conte et al. 2008, Carvalho et al. 2010). Besides the wide distribution and high population density (Gram & Sork 1999), the high genetic diversity may be also the outcome of historically high effective population size (see Galetti et al. 2013).

The absences of habitat loss and fragmentation effects on genetic diversity may be also the outcome of the relatively recently fragmentation of Atlantic Forest when considering species life cycle (Collevatti et al. 2001; see also Lowe et al. 2005 for a review). Also, the assessment of genetic variability using highly variable microsatellite loci may mask the reduction in heterozygosity because fragmentation would take too long to affect heterozygosity (Collevatti et al. 2001).

Moreover, habitat loss and fragmentation may affect genetic diversity and allelic richness only if fragmentation causes a population size reduction, i. e. if the fragmented patches delineate much smaller population than once existed in

continuous sites (Kramer et al. 2008). *Euterpe edulis* has a clumped distribution and high densities in most fragments. Thus, fragmentation and habitat loss will be barely detected if fragmentation in the studied region of Southeast Brazil maintained population sizes inside fragments.

Our results showed that inbreeding is important in shaping the genetic diversity in *E. edulis*. Despite the outcrossed mating system (t_m = 0.94) reported so far (Gaiotto et al. 2003), we found high inbreeding coefficients for all populations and overall populations. However, for self-compatible species, outcrossing rate may be highly variable among populations due to differences in pollinator availability and flowering phenology (Barret 2002). In addition F_{IS} was explained by matrix resistance cost and site isolation. We hypothesize that the results are most likely due to fragmentation and isolation leading to high frequency of mating between closely related individuals, as observed for other Neotropical tree species (e.g. *Caryocar brasiliense*, Collevatti et al. 2001; *Dipteryx alata*, Collevatti et al. 2013).

Moreover**,** genetic differentiation among pairs of populations (pairwise F_{ST}) was affected by matrix resistance and percentage of forest cover. Pairs of sites with high matrix resistance cost and low percentage of forest cover had higher $F_{ST.}$ This may be due to lower mobility of seed dispersers and pollinators (Jordano et al. 2007). In addition, the change in forest cover may also change the abundance and richness of seed dispersers and pollinators (Gonzalez et al. 2009, Uriarte et al. 2011, Martensen et al. 2012), decreasing gene flow and increasing genetic divergence among populations. Most fragments in the studied region of Atlantic Rainforest are small (<50 ha; Ribeiro et al. 2011) and may not support large populations of frugivorous birds, such as toucans and jacutingas (Willis 1979, Bierregaard et al. 1992, Silva & Tabarelli 2000). These animals are important to long distance dispersal (Nathan 2006), and their loss can limit the gene exchange among populations

Nevertheless, some pairs of sites with high matrix resistance cost and low percentage of forest cover had lower differentiation ($F_{ST,}$ Fig. 6) and lower inbreeding coefficient (F_{IS}, Fig. 5). These sites are mainly in Ipeúna and Iracemápolis landscapes (sites IP1 to IP3 and IR1 to IR3, respectively, see Table 1 and Supporting Information Table S7), which are characterized by very small fragments surrounded by sugarcane. We hypothesize that the small

fragments may have low carrying capacity for pollinators and seed dispersers, causing high frequency of movements of animals among fragments seeking for resources (e.g. White et al. 2002, Dick et al. 2003, Farwig et al. 2006), leading to high gene flow and low genetic differentiation among populations and low inbreeding of *E. edulis* in these landscapes.

Dick et al. (2003) showed that in disturbed habitat African honeybee (*Apis mellifera scutellata*) is the predominant pollinator of the Amazon tree *Dinizia excels,* carrying pollen grains up to 3.2 km. The region of Ipeúna and Iracemápolis landscapes is in the center of African honeybee dispersal in Brazil (Michener et al. 1975). Thus, honeybees may have been having an important role in gene flow in *E. edulis* after some generations since the release of African honeybee in Southeast Brazil, leading to a reduction in the genetic differentiation among *E. edulis* populations.

Geographic distance was one of the models with lower contribution for observed variation in pairwise F_{ST}. In fact, given the scale of our analysis, pure spatial distance may be less important than landscape resistance features in explaining genetic diversity and differentiation (see Spear et al. 2005 and Lange et al. 2012 for similar results). Thus, our study stressed the view that landscape structure along with geographic distance must be included in landscape genetic studies (see Manel et al. 2003 and Storfer et al. 2007 for reviews). Finally, our results also show that habitat loss and fragmentation effects on genetic diversity and polymorphism (H_e and *AR*) are less important, or harder to detect, than those effects on inbreeding (F_{IS}) and genetic differentiation (F_{ST}).

In conclusion, our study shows that matrix resistance has been affecting inbreeding and genetic differentiation in *E. edulis* populations. However, habitat loss and fragmentation, that are the mainly human impacts evaluated in most studies, had much less contribution in explaining the variation in F_{IS} and pairwise F_{ST} among sites in *E. edulis* populations. It highlights the importance in including landscape variables along with geographical distance in landscape genetics studies, such as the matrix resistance when seeking to understand the key ecological process associated to dispersal, as matrix can be shaping micro-evolutionary processes.

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Supporting Information

Table S1: Sampling locations of the 22 sites of *Euterpe edulis* in of Atlantic rainforest in São Paulo state, Southeast Brazil. N, number of individuals sampled.

Landscape	Sites	% forest cover around the focal fragment	Coordinates (Decimal degrees)		N
			Latitude	Longitude	
Caetetus	CA1	99	-22.3836	-49.6794	30
	CA2	99	-22.3928	-49.6899	30
	CA3	72	-22.3779	-49.6881	30
	CA4	29	-22.3864	-49.7274	31
Carlos Botelho	CB1	90	-24.0617	-47.9939	30
	CB2	87	-24.0627	-47.9886	30
	CB3	86	-24.0598	-47.9961	30
Corumbatai	CO1	28	-22.2691	-47.6576	14
	CO2	40	-22.2677	-47.6707	28
	CO3	24	-22.2695	-47.6451	28
	CO4	31	-22.2805	-47.6616	30
Dinamérica	DI1	49	-22.2933	-49.6275	30
	DI2	10	-22.2893	-49.6269	30
Ipeúna	IP1	2	-22.4141	-47.6642	26
	IP2	10	-22.4222	-47.6616	29
	IP3	7	-22.4156	-47.6727	27
Iracemápolis	IR1	23	-22.5575	-47.5811	30
	IR2	16	-22.542	-47.5655	30
	IR3	11	-22.5549	-47.5818	31
Tambaú	TA1	4	-21.6944	-47.3288	31
	TA2	11	-21.6969	-47.3225	31
	TA3	4	-21.6921	-47.3376	30

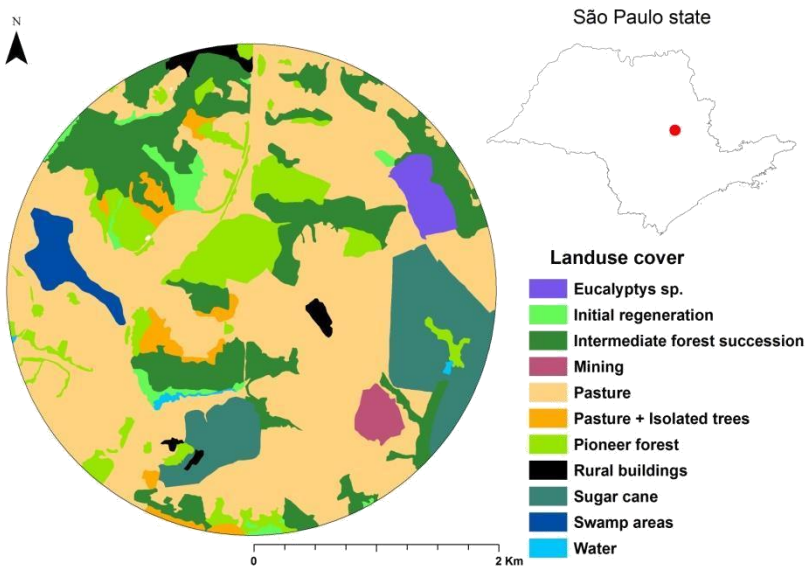

Fig. S1: Example of mapping classification of the landscapes with Atlantic Rainforest fragments and *Euterpe edulis,* in São Paulo state, Southeast Brazil. The map shows Corumbataí landscape, with 2 km of radius.

Supporting information S1: Details on the explanatory metrics calculation

1) Percentage of forest cover

To calculate the percentage of forest cover, we classified the fragments as advanced forest and intermediate forest succession. With the extension V-late of ArcGis version 9.2 (ENRI), we calculated the total area of forest in each landscape and the percentage of landscape forest cover.

2) Percentage of forest cover around focal site

To calculate the Percentage of forest cover around focal sites, we used a buffer of 500 meters around each focal site. With the package V-late, we calculated the total forest area (advanced forest and intermediate forest succession) in each landscape and its percentage.

3) Functional connectivity

To calculate the functional connectivity, we first classified the fragments in advanced or intermediate forest succession. Buffers of 50m were draw and the area of connected fragments was calculated using ArcGis version 9.2 (ENRI). We used measures of connectivity of 100 m for the dispersal distance reported to *Turdus* sp. (Jordano et al. 2007). *Turdus* sp. are the most common seed disperser *of E. edulis* in our landscape, as *Ramphastos* sp., *Procnias* sp.,

Pteroglossus sp. and *Aburria jacutinga* were lost in most studied sites (Galetti et al. 2013).

4) Matrix resistance

Loracs software (Pinto et al. 2012) simulates the least cost path for biological flow, using graphs theory (Urban & Keitt 2001). The software uses a resistance surface, i.e. a spatial layer that assigns values to each landscape feature. The values represent the degree in which the landscape features hold back or facilitate the moving and dispersal of individuals (Spear et al. 2010). There are three different ways to calculate resistance surface: field data, expert opinion and model optimization (Spear et al. 2010). We used expert opinion.

To make the resistance surface file, two ornithologists and one entomologist gave weights of resistance to each type of landscape features, considering each disperser and pollinator of *E. edulis*. We than performed a correlation analysis between the weights given by each expertise (Table S2). The correlation coefficients were high (above 0.6), showing that the answers were coherent.

Then, we performed a Principal Component Analysis (PCA, R Core Team 2012) with data set of each expertise, and ranked the values from 1 to 100, to obtain the resistance weight of each matrix. To run the simulations, we tested the maximum, minimum and mean weights of resistance (Table S3) between all pairs of sites inside the same landscape.

5) Site isolation

To calculate site isolation we calculated the geographic distance between the edges of each fragment pair using the extension Conefor of ArcGIS version 9.2 (ENRI). Further, we calculated the mean geographical distance.

Table S2: Correlation among weights of resistance for each type of landscape features, considering the seed dispersers and pollinators of *Euterpe edulis*, given by ornithologists. Bold numbers show that correlation coeficients between weights for the same landscape feature were higher than 0.6. Talb – *Turdus albicollis*, Tleu - *Turdus leucomelas,* Pnud - *Procnias nudicollis*, Pscu – *Pyroderus scutatus,* Psup – *Penelope superciliares*, Para – *Pteroglossus aracari*, Pbai – *Pteroglossus bailloni*, Rdic – *Ramphastos dicolorus*, Rvit – *Ramphastos vitellinus*, Ajac – *Aburria jacutinga*

	Talb	Tleu	Pnud	Pscu	Psup	Para	Pbai	Rdic	Rvit	Ajac
Talb	**0.93**	0.83	0.94	0.94	0.8	0.92	0.94	0.94	0.94	0.94
Tleu	0.53	**0.74**	0.5	0.5	0.59	0.55	0.5	0.5	0.5	0.5
Pnud	0.56	0.45	**0.64**	0.64	0.52	0.56	0.64	0.64	0.64	0.64
Pscu	0.77	0.65	0.83	**0.83**	0.7	0.78	0.83	0.83	0.83	0.83
Psup	0.81	0.72	0.87	0.87	**0.67**	0.79	0.87	0.87	0.87	0.87
Para	0.71	0.67	0.78	0.78	0.63	**0.74**	0.78	0.78	0.78	0.78
Pbai	0.71	0.55	0.77	0.77	0.63	0.7	**0.77**	0.77	0.77	0.77
Rdic	0.76	0.68	0.82	0.82	0.65	0.76	0.82	**0.82**	0.82	0.82
Rvit	0.57	0.53	0.64	0.64	0.44	0.56	0.64	0.64	**0.64**	0.64
Ajac	0.57	0.44	0.62	0.62	0.51	0.57	0.62	0.62	0.62	**0.62**

Table S3: Resistance weights assigned to each landscape feature. Weight I and II represent the value of resistance given by each expertise. AF -advanced forest, IF- intermediate forest succession, PF= pioneer forest, Eu – *Eucalyptus* sp., RB- rural buildings, IR- initial regeneration, CP- coffee plantation, ST- swamp areas with isolated trees, PT- pasture with isolated trees, Sw- swamp areas , Pa- pasture, SC – sugar cane, Mi – mining areas

	Weight I	Weight II	Minimum Weight	Maximum Weight	Mean Weight
AF	1	1	1	1	1
IF	1	37	1	37	19
PF	38	77	38	77	57.5
Eu	68	94	68	94	81
RB	94	66	66	94	80
IR	93	80	80	93	86.5
CP	86	83	83	86	84.5
ST	88	84	84	88	86
PT	89	81	81	89	85
Sw	100	86	86	100	93
Pa	100	86	86	100	93
SC	96	88	88	96	92
Mi	100	100	100	100	100

Table S4: Correlation values among explanatory metrics for landscape-site scale.

	Site Isolation	% of forest cover in 500m of radius	Functional connectivity	Matrix resistance cost	Matrix resistance length
Site Isolation	1				
% of forest cover in 500m of radius	-0.3	1			
Functional connectivity	-0.4	0.7	1		
Matrix resistance cost	0.1	-0.1	0.6	1	
Matrix resistance length	0.3	0.2	-0.2	0.1	1

Table S5: Correlation values among explanatory metrics for pairwise scale.

	% Forest cover	Matrix resistance cost	Matrix resistance length	Geographic distance
% Forest cover	1			
Matrix resistance cost	0.3	1		
Matrix resistance length	0.3	0.3	1	
Geographic distance	0.2	0.1	0.8	1

Table S6: Genetic characterization of the eight microsatellite loci based on 636 individuals of *Euterpe edulis* from 22 sites in Atlantic Rainforest remnants in São Paulo state, Southeast Brazil. *A*, number of alleles; H_e, expected heterozygosity; H_o, observed heterozygosity; *I*, probability of genetic identity following Chakravaratt and Li (1983); *Q*, probability of paternity exclusion following Weir (1996) ; *f,* inbreeding coefficient (* significant, p < 0.001)

Loci	***A***	***I***	***Q***	H_e	H_o	***F***
EE5	29	0.027	0.745	0.861	0.623	0.217*
EE8	22	0.054	0.647	0.796	0.640	0.135*
EE43	14	0.042	0.691	0.845	0.613	0.184*
EE52	25	0.007	0.872	0.936	0.643	0.277*
EE63	21	0.021	0.779	0.889	0.708	0.100*
EE25	25	0.011	0.843	0.922	0.680	0.227*
EE47	20	0.026	0.758	0.876	0.698	0.077*
EE45	20	0.018	0.799	0.899	0.546	0.318*
Overall loci		5.62E-14	0.9999941	0.88	0.645	0.185*

Table S7: Pairwise F_{ST} for 22 sites of *Euterpe edulis* in Atlantic Rainforest remnants of São Paulo state, Southeast Brazil. Bold numbers are F_{ST} that were not significant (p>0.05).

Sites	CO1	CO2	CO3	CO4	IP1	IP2	IP3	IR1	IR2	IR3	TA1	TA2	TA3	CB1	CB2	CB3	CA1	CA2	CA3	CA4	DA1
CO2	0.059																				
CO3	0.050	0.086																			
CO4	0.093	0.161	0.095																		
IP1	0.071	0.086	0.056	0.090																	
IP2	0.057	0.089	0.071	0.086	0.036																
IP3	0.057	0.078	0.067	0.102	0.038	0.032															
IR1	0.033	0.096	0.064	0.073	0.075	0.060	0.058														
IR2	0.035	0.083	0.054	0.085	0.063	0.073	0.072	0.047													
IR3	0.048	0.093	0.066	0.107	0.075	0.072	0.081	0.046	0.020												
TA1	0.111	0.166	0.121	0.190	0.154	0.152	0.142	0.137	0.125	0.137											
TA2	0.129	0.163	0.101	0.176	0.097	0.122	0.137	0.141	0.115	0.123	0.124										
TA3	0.062	0.122	0.083	0.103	0.093	0.097	0.105	0.083	0.041	0.067	0.118	0.095									
CB1	0.082	0.157	0.132	0.182	0.128	0.130	0.135	0.098	0.093	0.109	0.169	0.191	0.152								
CB2	0.072	0.138	0.117	0.168	0.108	0.102	0.110	0.092	0.076	0.089	0.170	0.155	0.125	0.021							
CB3	0.077	0.139	0.130	0.180	0.126	0.121	0.131	0.094	0.077	0.092	0.175	0.182	0.132	0.015	**0.002**						
CA1	0.063	0.141	0.090	0.130	0.113	0.103	0.110	0.069	0.058	0.062	0.131	0.150	0.087	0.079	0.080	0.081					
CA2	0.086	0.153	0.107	0.149	0.125	0.113	0.135	0.098	0.085	0.074	0.166	0.141	0.099	0.120	0.108	0.116	0.031				
CA3	0.079	0.144	0.103	0.137	0.113	0.114	0.126	0.083	0.066	0.054	0.163	0.146	0.095	0.093	0.088	0.090	0.017	0.026			
CA4	0.087	0.150	0.103	0.154	0.116	0.099	0.093	0.096	0.095	0.095	0.157	0.160	0.111	0.122	0.110	0.126	0.055	0.068	0.074		
DA1	0.083	0.151	0.109	0.160	0.123	0.112	0.127	0.094	0.082	0.068	0.172	0.149	0.097	0.090	0.079	0.085	0.024	0.033	0.015	0.069	
DA2	0.107	0.182	0.142	0.176	0.159	0.137	0.157	0.112	0.128	0.110	0.204	0.197	0.140	0.126	0.126	0.135	0.039	0.053	0.046	0.085	0.044

Conclusão

Nossos estudos mostraram que a distribuição da variabilidade genética do *Euterpe edulis* está atrelada a diversos fatores, como diferentes tipos florestais e áreas mais adequadas para a ocorrência da espécie. No entanto, apesar da variabilidade genética dessa espécie se manter alta na maioria das áreas estuda, há indícios que impactos antrópicos como redução de habitat e fragmentação estão levando a perda da variabilidade e aumento da diferenciação genética. Nossos estudos também mostraram a importância de incluir variáveis de características da paisagem, como resistência da matriz, para entender processos ecológicos chave como dispersão e polinização. Portanto, para conduzir um eficiente plano de conservação da espécie é importante levar em conta não só o impacto humano, como perda de habitat e fragmentação, como também a heterogeneidade de habitat.