

# Climatic stability and contemporary human impacts affect the genetic diversity and conservation status of a tropical palm in the Atlantic Forest of Brazil

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**Abstract** Understanding how historical and current environmental suitability and human impacts affect the genetic diversity on a large scale is essential to species management planning. However, most studies in conservation genetics are carried out at a local or regional scale and rarely on broad spatial scales such as an entire biome. We evaluated the relative contribution of historical and current environmental suitability, current landscape features and human impacts to explain genetic diversity, allelic richness and inbreeding variation among populations, using *Euterpe edulis* and the Atlantic forest as the model system. We fitted linear mixed models within a multiple competing hypotheses approach with model selection based on Akaike's Information Criteria. We showed that overall genetic diversity was lower in sites with absence of large seed dispersers and higher in sites with historically stable climate. Both seedling and adults showed to be negatively influenced by human impact factors; with adults mainly affected by the reduction of forest cover while seedlings by the loss of large seed dispersers. Thus, the current pattern

of genetic diversity in *E. edulis* is the result of historical instability during the mid-Holocene and recent anthropogenic impacts, mainly those that affect important ecological process such as seed dispersal. Thus, an efficient plan for species conservation must account for human impacts and environmental suitability and also assess the genetic diversity of seedlings and adults in fragmented landscapes.

**Keywords** Ecological niche modeling · Defaunation · Human impacts · Conservation genetics · *Euterpe edulis* · Atlantic Forest

## Introduction

Understanding how past and current environmental suitability and human impact factors affect patterns of genetic diversity and biodiversity distribution is a challenge for both ecologists and biogeographers (Gaston 2000). The maintenance of genetic diversity in natural populations is essential for species management planning (Hughes et al. 2008), since species with low genetic diversity may be less likely to cope with environmental changes and therefore may become endangered or face extinction (Hoffmann and Willi 2008). Although genetic diversity has a fundamental role in species persistence and adaptation, few studies have reported the role of environmental suitability and human impacts in genetic diversity on a broad scale (Diniz-Filho et al. 2009; Ortego et al. 2012).

Several historical and contemporary factors may influence genetic diversity and inbreeding in natural populations. Historical factors related with climate and geological events may change the habitat suitability for species establishment or persistence and may therefore imprint a signal in the species genetic pool over time (Hewitt 2000).

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The Quaternary climatic oscillation, for example, might have affected species genetic diversity due to the dynamics of population's expansion and contraction (Gugger et al. 2013). Population range contraction may decrease effective population size, leading to population bottlenecks and genetic drift, with the consequent loss of genetic diversity (Pauls et al. 2013). Loss of genetic diversity may also occur during population expansion into new habitats (Pauls et al. 2013) due to founder effects or recovery from population bottlenecks, since only a part of the original genetic diversity moves or persists into new habitats (Pauls et al. 2013). The colonization of new habitats during expansion can result in a high genetic admixture of immigrants arriving from different populations (Ortego et al. 2015), which could either increase genetic diversity due to heterosis or reduce genetic diversity if outbreeding depression occurs. Finally, sites with high environmental suitability and stable climate over time may preserve high genetic diversity in populations (Collevatti et al. 2014).

Contemporary factors that may affect genetic diversity include processes occurring at ecological scales and relate strongly with human activities (Miraldo et al. 2016). Global changes induced by human activities including climate change and conversion of land covers may affect species richness, abundance, and several key ecological processes (Fahrig 2003), such as pollination (González-Varo et al. 2009), seed dispersal (Uriarte et al. 2011) and animal movement (Eycott et al. 2012). Fragmentation and habitat loss are two factors identified as the main anthropogenic threats to genetic diversity (Lowe et al. 2005; DiBattista 2007; Aguilar et al. 2008). These anthropogenic threats may lead to a drastic reduction of population sizes, and consequently of effective population size (Frankham et al. 1999; Andersen et al. 2004). The probability of mating between closely related individuals may increase in small populations and, together with genetic drift, lead to a substantial reduction in genetic diversity (Breed et al. 2012). In these human-dominated scenarios, local extinction of medium- and large-body sized animals (i.e., defaunation; Dirzo and Miranda 1991) affects the composition and ecological functions of animal communities (Wright 2003). Seed dispersal is amongst the many ecological roles these animals provide to the community. Large-sized frugivores are important for long distance seed dispersal because they can move seeds hundreds of meters away from the mother plant. Therefore, these animals can promote gene flow and increase genetic diversity in plant populations (García et al. 2007; Jordano et al. 2007).

Although many studies focus separately on the effects of historical climate oscillation and human disturbances on genetic diversity, few evaluate the relative contribution of these historical and contemporary effects in the same system (Walter et al. 2012). Understanding how historical

events impact genetic diversity is important to predict whether populations are able or not to persist under future scenarios of environmental change (Pauls et al. 2013). In addition, evaluating the effects of contemporary factors like habitat fragmentation on genetic diversity helps identifying actions to prevent genetic erosion or to rescue genetic diversity of impacted populations. Therefore, quantifying the effects of historical and contemporary factors on species genetic pool may help design strategies for species and landscape conservation.

Large spatial and temporal scale studies are necessary to better understand how the historical and current factors shape genetic diversity across the distribution of natural populations and contribute to efficient species conservation planning (Huber et al. 2010). Large-scale studies can act as natural experiments to investigate historical climate effects on biodiversity because distinct sites may be differently affected by the oscillation in climate. Due to time lag effects, adult plants and seedlings may respond in a different way to human impacts (Van Geert et al. 2008). When estimated using microsatellite markers, the genetic diversity of adults of perennial plants often responds to past landscape conditions but not to recent habitat changes (Collevatti et al. 2001; Kramer et al. 2008). When evaluating ongoing processes, such as dispersal events culminating in gene flow, it is more appropriate to assess genetic variability in early recruitment stages (e.g., seed and seedlings in plants) rather than adults (Kramer et al. 2008).

The Atlantic forest biome has an extensive geographic range, presenting a wide variation in climate, topography and vegetation along its distribution (Ribeiro et al. 2011). It is also one of the most threatened ecosystems in South America, mainly due to anthropogenic disturbances (Rands et al. 2010; Tabarelli et al. 2010). Its current extension constitutes only 12% of its original 150 million hectares (Ribeiro et al. 2009). The heart of palm (*Euterpe edulis*, Arecaceae), a threatened Atlantic forest species, was once one of the dominant palms in this ecosystem (Henderson et al. 1997). The species is present in different vegetation types ranging from dense mountain rain forests to seasonally dry forests, where it is restricted to wet microhabitats. The edible meristem (heart of palm), obtained mainly by illegal exploitation, is used as source of raw material for food industries (Galetti and Fernandez 1998). *Euterpe edulis* is a monoic species with a predominantly outcrossed mating system with low amount of selfing (Gaiotto et al. 2003). Its flowers are mainly pollinated by small bees (Reis et al. 2000). The ripe fruits constitute an important food resource for animals, including more than 50 species of birds and mammals (Galetti et al. 2013). Several population genetics studies of *E. edulis* have been carried out at local or regional scales. Metadata combining the already published genetic diversity data may contribute to the

understanding of large-scale patterns (Lowe et al. 2005; DiBattista 2007) of *E. edulis*.

Here, we address the distribution of genetic diversity of *E. edulis* and evaluate whether past and current environmental variables and human-induced changes can explain variation among localities, using published data derived from microsatellite loci. First, we built ecological niche models for *E. edulis* in three different time periods (the Last Glacial Maximum, the mid-Holocene and the present-day) to understand how changes over time in habitat suitability for species establishment may have affected genetic diversity and inbreeding. Second, we evaluated the relative contribution of climatic habitat suitability in the past and in the present-day, together with current landscape features modified by human activities to explain the patterns in genetic diversity of *E. edulis*. We expect to find high genetic diversity in areas of high climatic stability and high habitat suitability. In addition, we expect to find stronger effects of human-modified environmental factors on seedlings than in adults, given that adults may have not had enough time to respond to the recent intensification of environmental changes caused by humans, mainly forest fragmentation and functional extinction of seed dispersers in the Atlantic Forest.

## Methods

### Literature search

We surveyed publications of population genetic studies on *E. edulis* using the following databases: Scielo (<http://www.scielo.org>), Web of Science (<http://www.webofscience.com>), Scopus (<http://www.scopus.com>), and Google Scholar (<http://www.scholar.google.com.br>). The survey covered all publications available from 2001 to November 2015. We used the most frequent keywords in the area: “population genetics”, “*E. edulis*”, “microsatellites”, “genetic diversity”, “conservation genetics”, and “heart of palm”. We included only publications comprising populations from the northeast to southeast Brazilian Atlantic coast that used microsatellites as molecular markers (Fig. 1).

### Genetic diversity response variables

Three genetic parameters were used as response variables in our analyses: the inbreeding coefficient ( $f$ ); the genetic diversity, measured by expected heterozygosity ( $H_e$ ) and allelic richness ( $AR$ ). We chose these genetic parameters because they are present in most publications (Supplemental Information, Table A1) and are frequently used in

conservation genetics studies as surrogates for population evolutionary potential.

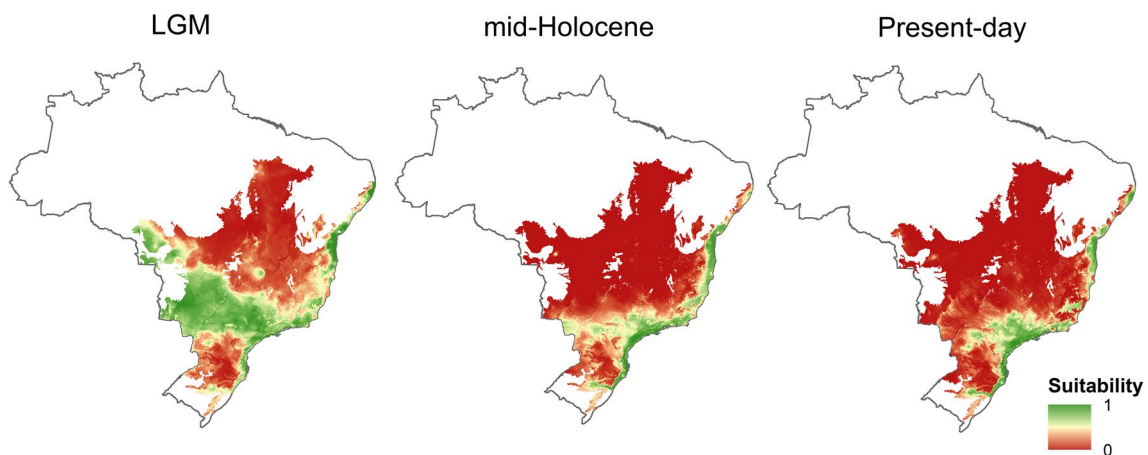
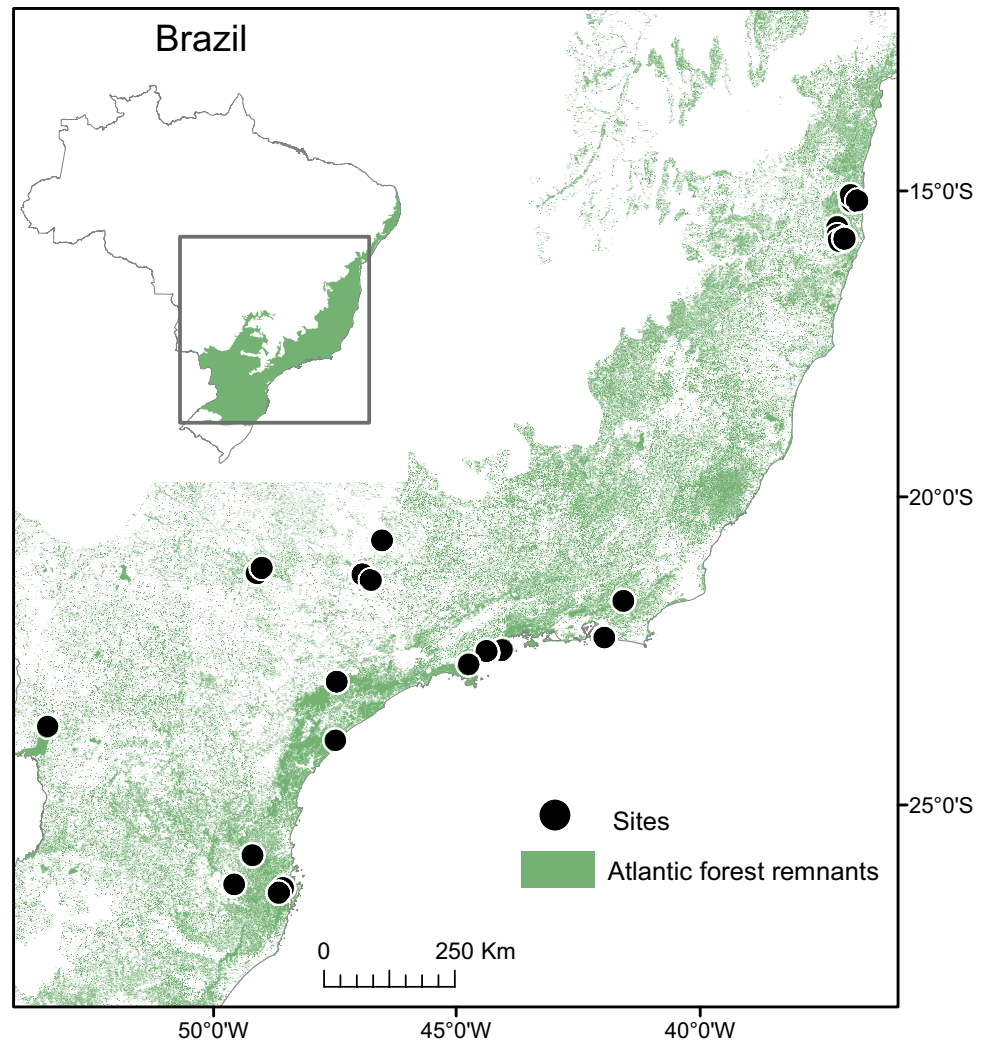
### Predictive models

We used three groups of covariates to explain genetic diversity: (i) human-induced; (ii) climatic habitat suitability; and (iii) stability of climatic habitat suitability. Human-induced covariates were: (a) percentage of forest cover and (b) loss of large-body frugivores (i.e., defaunation). Climatic habitat suitability was measured through ecological niche modeling (ENM hereafter) for each of the time periods (the Last Glacial Maximum, the mid-Holocene and the present-day). We also measured the cumulative suitability as the sum of climatic habitat suitability over the three periods. The climatic stability was calculated as the difference between past and present climatic habitat suitability.

To quantify the covariates for modeling genetic diversity, we drew a buffer area with a 2 km radius around each of the 57 selected study sites from the surveyed literature. We chose this radius because the foraging distance of potential pollinators, such as *Plebleia droryana* and *Trigona spinipes*, can reach up to 540 and 840 m, respectively (Zurbuchen et al. 2010). Furthermore, seed dispersal distances by large-body bird species that are taxonomically related to the dispersers of *E. edulis* are likely to be shorter than 600 m (Holbrook 2011). We used the SOS Mata Atlântica map (2005, <http://mapas.sosma.org.br/>) and the ArcGIS 9.2 software (ENRI) to calculate the total area and the percentage of forest inside each 2 km-radius buffer area. Defaunation was defined as the absence or very low abundance of Ramphastidae (e.g., toucans and toucanets) and Cotingidae (e.g., bellbirds) species within the buffer area and was classified as a binary variable: defaunated (0) or non-defaunated (1). Species of these families are important long distance dispersers for *E. edulis* seeds (Holbrook 2011; Galetti et al. 2013). To assign the defaunation status of each site, we characterized the avian seed dispersal assemblage using the Wikiaves website (<http://www.wikiaves.com.br>) and available literature (Galetti et al. 2013; Morante-Filho et al. 2015).

To assess the climatic suitability of the study area we carried out ecological niche modeling of *E. edulis* combining species occurrences and climatic variables. A total of 229 occurrence records (Fig A1 in Supplementary material) were obtained from Species Link (<http://www.splink.org.br>), Jardim Botânico do Rio de Janeiro (<http://www.jbrj.gov.br>) and Biota Fapesp (<http://www.biota.org.br/>). All records were carefully checked for taxonomic reliability (i.e., synonymous and/or misidentification and duplicates). We carefully restricted our modeling area to encompass only Cerrado and Atlantic forest biomes (Fig. 2).

**Fig. 1** Distribution of the 57 sampled sites with genetic information for *Euterpe edulis* across the Brazilian Atlantic forest biome in Brazil



**Fig. 2** Maps of mean climatic suitability across the ten ecological niche models (ENMs), five Atmosphere–Ocean General Circulation Models (AOGCMs) and three time periods (at the LGM, mid-Holocene and present, respectively) for *Euterpe edulis* in Brazil

The environmental space required for the ENMs was characterized by five bioclimatic variables: temperature seasonality, maximum temperature of the warmest month,

precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter together with elevation and soil classes (<http://www.embrapa.br>).

Climatic variables were selected out of the 19 bioclimatic variables (Worldclim; <http://worldclim.org>; Hijmans et al. 2005) after performing a factor analysis with Varimax rotation to minimize collinearity among the variables when building the distribution models (For details on selection of variables see Supplementary material, Table A2). We derived distribution models using layers from the pre-industrial period (representing current conditions; 0 ka), the mid-Holocene (6 ka) and the Last Glaciation Maxima (LGM, 21 ka). Current models were then projected onto three Atmosphere–Ocean General Circulation Models (AOGCMs; CCSM4, MIROC-ESM and MPI-ESM-P) obtained from Coupled Model Intercomparison Project Phase 5 (CMIP5; <http://cmip-pcmdi.llnl.gov/cmip5/>). We assumed soil and elevation as constraint variables (constant throughout time). All layers were used in a spatial resolution of 2.5 arc-min (ca. 5 × 5 km).

A total of 200 spatially independent localities were used for the models. ENM was carried out with biomod2 in R 3.1.2 (Thuiller et al. 2009). Six different algorithms were used (see Supplementary material for model parameterization): Artificial Neural Networks (ANN), Generalized Additive Models (GAM), Generalized Linear Models (GLM), Generalized Boosted Models (GBM), Random Forest (RF), and maximum entropy (MAXENT; Phillips and Dudík 2008). Usually ENM requires presence-absence data for model fitting and testing; however, there are not reliable absences available. Therefore, we chose to generate pseudo-absences randomly across the whole area (Ferrer et al. 2002), excluding cells with presences to ensure a complete sampling of the environmental space and minimum extrapolation when projecting to different historical period. To maximize model performance, pseudo-absences were weighted to ensure maintaining prevalence equal to 0.5 (Barbet-Massin et al. 2012). We used random data partitioning (80% training, 20% testing) and five repetitions for each model to assess model stability due to the absence of independent testing data. We assessed model accuracy through the calculation of the True Skill Statistic–TSS (Allouche et al. 2006) and the area under the receiver curve–AUC (Fielding and Bell 1997) (Table A3 in Supplementary material). Since results might differ among different algorithms, we performed an ensemble modeling (Araújo and New 2007) to calculate a consensus map that included only models with a TSS > 0.7 and an AUC > 0.75 and the resulting map was weighted by the individual model TSS value. Thus we generated a surface representing the suitability values for the occurrence of the species across our study area for both current and past climatic periods.

To access climatic stability we calculated the difference between the past (6 and 21 ka) and current (0 ka) suitability within the 2 km radius buffers for each site. Positive values

indicate that current climatic suitability is lower than in the past (contraction population range) and negative values show that the current climatic suitability is higher than in the past (expansion population range). Zero value indicates that the site is climatically stable, which could either be associated with high environmental suitability or not. To account for the cumulative suitability over time, we also calculated the sum of suitability in the three different time periods.

### Statistical analyses

We investigated the effects of the explanatory variables (i.e., defaunation status, percentage of forest cover, climatic habitat suitability in the present-day, cumulative climatic habitat suitability, stability from the mid-Holocene to present-day and stability from the LGM to present-day) on the three genetic parameters (i.e.,  $f$ ;  $H_e$ ,  $AR$ ). We fitted full models only for adults, only for seedlings and adults and seedlings combined for each genetic parameter using a linear mixed effects and the maximum-likelihood method using the R package lme4 (Bates et al. 2015), which is an adequate way to assess the influence of fixed effects given random structure. Defaunation status, percentage of forest cover, current climatic habitat suitability, cumulative climatic habitat suitability, climatic stability from the mid-Holocene to present-day and climatic stability from the LGM to present-day were considered as *fixed effects*. Ontogenetic stage (adults or seedlings) and “study” were included as *random effects* while sample size of each site was included as a *weight* parameter in all models. The “study” was included to take into account the difference in the set of microsatellites markers and in the number of populations and individuals sampled (Table A1). We assumed that these factors might influence the estimation of genetic parameters. The ontogenetic stage (adults and seedlings) was included as *random effects* only in the model that included all individuals. After fitting the full model, we fitted nested models with all possible combinations of the fixed effects.

Because the effect of historical and current factors on genetic variables tends to be complex and dependent on the interaction of diverse factors (Boscolo and Metzger 2011), we used a model selection with multiple competing hypotheses approach (Burnham and Anderson 2002). To select the best model, we used the Akaike Information Criteria (AIC), where the model with the lowest AICc (AIC corrected by sample size and number of parameters) (Burnham and Anderson 2002) was considered as the more plausible to explain observed patterns. Delta AICc ( $\Delta AICc_i$ , where  $i$  represents each model) was calculated as the difference between AICc for the model  $i$  and the smallest observed AICc. We determined Akaike’s weight

of evidence (wAICc) representing the relative contribution of model  $i$  to explain the observed pattern, given a set of competing models (Burnham and Anderson 2002). Models with  $\Delta\text{AICc} < 2$  were considered as equally plausible to explain the observed pattern (Burnham and Anderson 2002). We also carried out a model averaging approach to compute the parameter average from all equivalent models ( $\Delta\text{AICc} < 2$ ) and the significance of the estimated parameter values associated with each explanatory variable (Burnham and Anderson 2002). All analyses were performed using the *MuMIn* packages implemented in R version 3.0.2 (Barton 2016). We also analyzed if seedlings have on average lower levels of genetic diversity than adult populations.

To account for the presence of spatial autocorrelation, we ran linear mixed models with the restricted maximum-likelihood method with different spatial covariance structures (Gaussian, exponential and spherical) and compared them to a model without a spatial covariance structure. We ran these models by fitting all explanatory covariates as *fixed effects* and the study and ontogenetic stage as *random effects*.

## Results

### Literature search

We obtained eight publications, which accounted for 61 study sites. However, four sites were excluded from the analysis because they were outside of the Atlantic Forest biome; in the end, we used 57 sites (Fig. 1 and Supplemental Information Table A1). Most populations of *E. edulis* in the Atlantic forest biome showed high genetic diversity (Supplemental Information Table A1).  $H_e$  ranged from 0.57 to 0.86, and  $AR$  varied from 3.6 to 15.1. However, many populations showed high  $f$  value (Supplemental Information Table A1).

### Climatic suitability and stability models

A total of 30 models were generated by the ENMs. From those, 83% were considered good under AUC criteria (Mean AUC, Table S3). The map of the modeled distribution under present conditions mostly agrees with the known current distribution for the species. The consensus map reveals suitable areas for the occurrence of the species across the coastal part of Brazil, from Pernambuco state in the northeast to Santa Catarina state in the south (Fig. 2). The region of higher climatic suitability coincides with the core area of Atlantic rain forests (Fig. 2) and shows the preference of *E. edulis* for hot and humid climates. Hindcasting to the LGM and the mid-Holocene showed a retraction of suitable areas through time, especially in areas

across central Brazil. The differences between past and current suitability values show a strong variation along the geographic distribution of the Atlantic Forest, with a reduction in habitat suitability in central Brazil during the mid-Holocene (i.e., retraction) and high stability and suitability since the LGM in areas along the coastal part of Brazil (Fig. 2; Table A1).

### Effects of historical and current factors on genetic diversity

The results of the model selection indicated that models without a spatial covariance structure were considerably better for modeling  $H_e$ ,  $AR$  and  $f$  than those with spatial covariance structures (Gaussian, exponential and spherical) (Supplementary material Table A4). Considering all individuals, variation in  $H_e$  and  $AR$  were best explained by the lack of large seed dispersers (Table 1). Defaunated sites presented lower  $H_e$  and  $AR$  than non-defaunated sites (Fig. 3a, b). The inbreeding coefficient ( $f$ ) was best explained by climatic stability from the mid-Holocene to present-day (Table 1). The inbreeding coefficient was lower in areas with decreasing suitability values over time (habitat contraction) and was higher in areas under expansion (Fig. 3c).

We found that seedlings have on average lower levels of allelic richness than adult individuals ( $t = -2.49$ ,  $p = 0.01$ ), however we did not find differences in  $H_e$  and  $f$  between ontogenetic stages ( $t = -0.03$ ,  $p = 0.97$ ;  $t = -1.5$ ,  $p = 0.12$ , respectively). Considering only adults, variation of  $AR$  could not be explained by any of our competing models (Table 1). On the other hand,  $H_e$  was explained by climatic stability from the mid-Holocene to present-day (Table 1). Lower values of  $H_e$  were associated with populations in areas where climatic suitability decreased from the mid-Holocene to present-day (Fig. 3d). Nevertheless, the genetic diversity ( $H_e$ ) remained high in areas under expansion or that were consistently suitable over time (Fig. 3d). Variation of  $f$  was best explained by the percentage of forest cover and by climatic stability from the mid-Holocene to present-day (Table 1). Populations in landscapes with higher percentage of forest cover showed lower  $f$  than populations in landscapes with lower forest cover (Fig. 3e). The model also shows that there is a decrease in the inbreeding coefficient when there is a retraction from suitable areas through time (positive climatic stability, Fig. 3f). Likewise, the inbreeding coefficient ( $f$ ) increases in areas undergoing expansion over time (Fig. 3f). Considering only seedlings, variation in  $H_e$  was not explained by any of our competing models (Table 1); however,  $f$  was best explained by the climatic stability from the mid-Holocene to present-day (Table 1), as found for adults (Fig. 3g). Finally, defaunation

**Table 1** Summary statistics for the model-averaging used to explain the genetic diversity pattern in populations of *Euterpe edulis* from 57 sites, distributed along the Brazilian Atlantic Rainforest

Parameter	$H_e$		$f$		$AR$	
	Model averaged (SE)	p-value	Model averaged (SE)	p-value	Model averaged (SE)	p-value
All individuals						
Defaunation*	<b>0.29 (0.13)</b>	<b>0.03</b>	–	–	<b>0.24 (0.08)</b>	<b>0.00</b>
% Forest cover	–	–	–0.13 (0.09)	0.18	–0.05 (0.05)	0.28
Current climatic suitability	–0.02 (0.23)	0.93	–0.12 (0.08)	0.17	–0.22 (0.11)	0.06
Climatic stability Holocene-present*	–	–	<b>–0.29 (0.14)</b>	<b>0.04</b>	–	–
Climatic stability LGM-present	0.15 (0.09)	0.10	–0.11 (0.11)	0.31	–	–
Cumulative suitability	0.22 (0.14)	0.12	–0.09 (0.08)	0.29	0.27 (0.16)	0.09
Adults						
Defaunation	0.48 (0.26)	0.09	–	–	0.28 (0.19)	0.17
% Forest cover*	–	–	<b>–0.57 (0.14)</b>	<b>0.00</b>	–0.16 (0.12)	0.21
Current climatic suitability	–	–	–	–	–0.36 (0.17)	0.06
Climatic stability Holocene-present*	<b>–0.28 (0.13)</b>	<b>0.04</b>	<b>–0.33 (0.14)</b>	<b>0.03</b>	–	–
Climatic stability LGM-present	–	–	–	–	–	–
Cumulative suitability	0.22 (0.12)	0.08	–	–	0.35 (0.20)	0.09
Seedlings						
Defaunation*	0.15 (0.18)	0.43	–	–	<b>0.39 (0.11)</b>	<b>0.00</b>
% Forest cover	0.09 (0.10)	0.39	–	–	–0.01 (0.06)	0.86
Current climatic suitability	0.11 (0.08)	0.23	–0.15 (0.09)	0.11	0.08 (0.13)	0.55
Climatic stability Holocene-present*	–0.19 (0.18)	0.31	<b>–0.45 (0.17)</b>	<b>0.01</b>	0.07 (0.11)	0.53
Climatic stability LGM-present	–	–	–0.22 (0.12)	0.08	–0.03 (0.07)	0.65
Cumulative suitability	0.11 (0.10)	0.29	–0.12 (0.10)	0.24	–0.01 (0.17)	0.92

Model averaged indicates the model-averaged estimates for fixed effects and SE the standard errors, p-value, p value for estimate coefficient values;  $H_e$  expected heterozygosity;  $AR$  allelic richness;  $f$  inbreeding coefficient. Effects where p value < 0.05 are highlighted by stars (\*) and in bold numbers

(Table 1) explained variation in  $AR$ . Non-defaunated sites presented higher  $AR$  than defaunated sites (Fig. 3h).

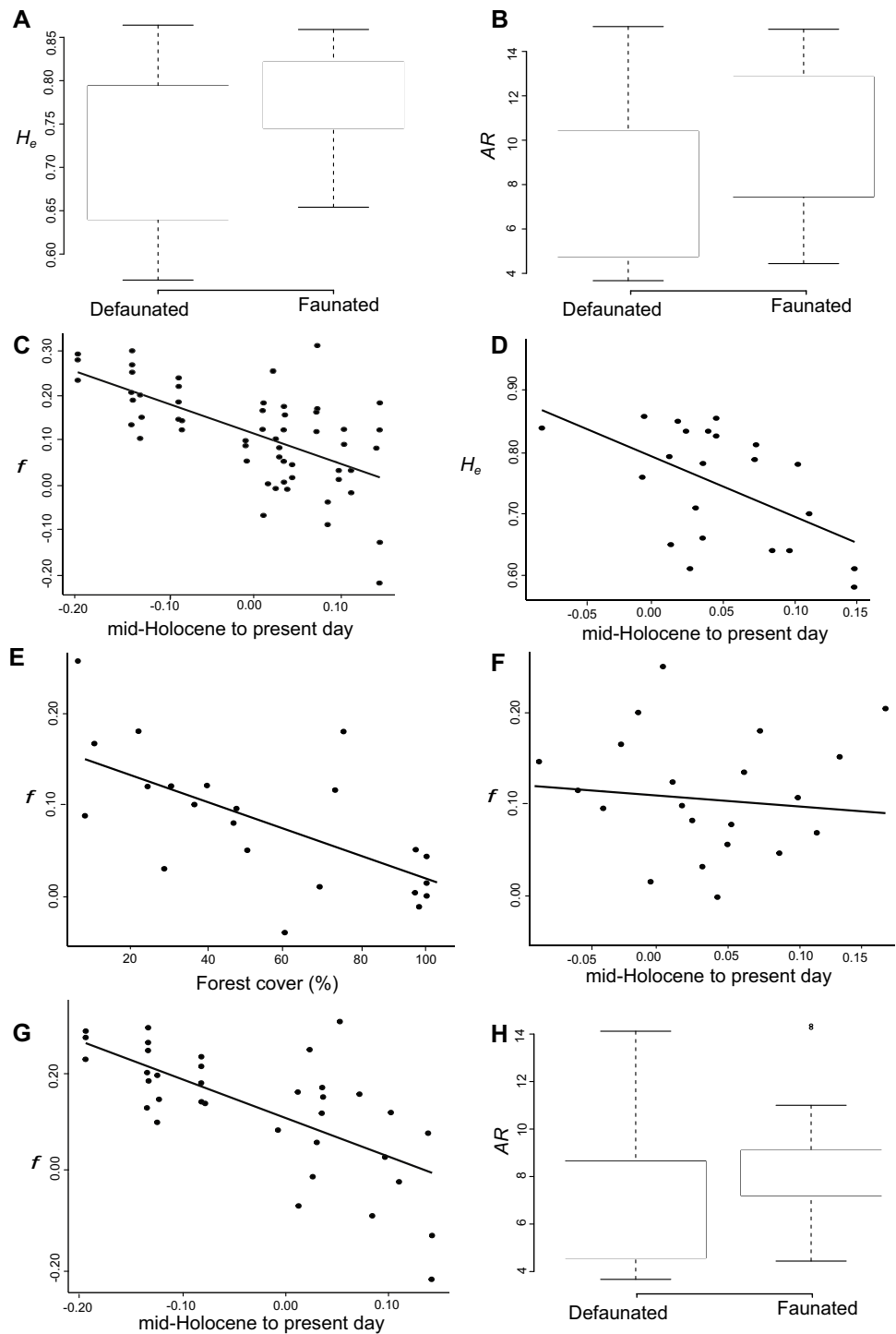
### Discussion

Our results show a retraction in the suitable areas for *E. edulis* through time and that the current pattern of *E. edulis* genetic diversity is the result of such historical population retraction and the current human impact. Combined effects of climatic habitat suitability, lack of large seed dispersers and habitat loss and fragmentation affected genetic diversity of heart of palm populations. Nevertheless, these observed patterns were not consistent across ontogenetic stages, as adults and seedlings are affected by different anthropogenic factors. The complex patterns found between different genetic parameters with historical environmental variables and human impacts indicate that it may be difficult to disentangle the processes involved in the origin and maintenance of genetic diversity.

The consensus map of climatic habitat suitability in the present-day (0 ka), mid-Holocene (6 ka BP) and LGM

(21 ka) revealed a contraction in climatically suitable areas for *E. edulis* from central sites towards the Brazilian Atlantic coast. Our ENM results showed that the potential distribution of *E. edulis* is currently narrower than it was in the mid-Holocene and in the LGM. The strong reduction in suitability during the mid-Holocene might have caused population extinction at least in part of the *E. edulis* distribution. Nevertheless, some areas, mainly in the Brazilian Atlantic coast, have been climatically stable through time and might have been important climatic refugia for *E. edulis*. In fact, we found that climatically stable sites can harbor a high amount of genetic diversity in heart of palm populations. Other studies also found that the Brazilian Atlantic coast may have been refuge for natural populations during the Quaternary climatic oscillation (Carnaval et al. 2009; Leite et al. 2016). *Euterpe edulis* populations in these refugia with stable or increasing suitability over time presented higher diversity compared to populations in areas with decreasing suitability since the mid-Holocene. Higher genetic diversity in populations under recent expansion probably reflects the admixture of immigrants arriving from different populations and also the maintenance of

**Fig. 3** Relationship between genetic parameters and the main explanatory factors in 57 study sites of *Euterpe edulis* across the Atlantic forest in Brazil. **a** genetic diversity ( $H_e$ ) and defaunation for all individuals, **b** allelic richness ( $AR$ ) and defaunation for all individuals, **c** inbreeding coefficient ( $f$ ) and climatic stability from mid-Holocene to present-day for all individuals, **d** genetic diversity ( $H_e$ ) and climatic stability from mid-Holocene to present-day for adults, **e** inbreeding coefficient ( $f$ ) and percentage of forest cover for adults, **f** inbreeding coefficient ( $f$ ) and climatic stability from mid-Holocene to present-day for adults, **g** inbreeding coefficient ( $f$ ) and climatic stability from mid-Holocene to present-day for seedlings, and **h** allelic richness ( $AR$ ) and defaunation for seedlings



large effective population sizes (Ortego et al. 2015). On the other hand, range retractions due to low environmental suitability might lead to population bottlenecks, with loss of individuals and genetic diversity (Pauls et al. 2013).

Conversely, our results show that populations of both adults and seedlings in areas under recent expansion of climatic suitability have higher inbreeding coefficients. The high expected heterozygosity ( $H_e$ ) despite high inbreeding

coefficients ( $f$ ) observed in some populations may indicate assortative mating between *E. edulis* palms most likely due to short-distance pollination, spatial distribution of plants, fine-scale spatial genetic structure or flowering patterns (Ghazoul 2005). Another possible explanation is that selfing may occur more frequently to favor reproductive assurance, which may be advantageous in expanded populations (Arnaud-Haond et al. 2006; Pujol et al. 2009). Thus, we



suggest that populations in areas with expanded range are an admixture of individuals from different populations, yet with production of inbred descendants. It could be the result of increased reproductive assurance due to selfing and increased biparental inbreeding due to assortative mating.

On the other hand, we found low inbreeding coefficients in populations that have recently contracted. The reduction of habitat suitability may lead to a reduction of population size and density. Some authors argue that population density is critical when the distance between individuals leads to changes in the foraging behavior of pollinators (Ghazoul 2005; Côrtes et al. 2013). Low population density and higher distance among individuals may increase pollen dispersal distance due to high mobility of pollinators in search for resources (Côrtes et al. 2013). Low inbreeding coefficients may also be the result of loss of homozygous individuals due to lower survival success (i.e., inbreeding depression, Keller and Waller et al. 2002), mainly in low suitable habitats. Thus, we suggest that while contracting populations lose genetic diversity due to bottleneck effects, inbreeding remains low due to higher mobility of pollinators in low density populations or higher loss of homozygous individuals in unsuitable habitats.

Along with climatic suitability, anthropogenic factors may also affect the genetic diversity of *E. edulis*. Despite the high fragmentation and habitat loss *E. edulis* populations still present high genetic diversity within the Atlantic forest (Gaiotto et al. 2003; Conte et al. 2008; Carvalho et al. 2015). The high historical effective population size (Galetti et al. 2013) and wide historical climatic habitat suitability distribution may have led to high genetic diversity in currently small and isolated populations. However, we did find significant and negative effects of defaunation on the genetic diversity ( $H_e$ ) and allelic richness of this species. The loss of large-body seed dispersers may result in the loss of very important ecological functions for plants that include the colonization of new habitats and connectivity between isolated populations (Pacheco and Simonetti 2000; Markl et al. 2012). Connectivity between populations is important for maintaining gene flow and, consequently, large effective population size and genetic diversity (Young et al. 1996). Moreover, habitat loss increased inbreeding levels in *E. edulis*. Habitat loss may affect the composition, abundance and behavior of pollinators communities, which in turn can limit pollination by increasing the probability of selfing and mating between closely related individuals. In addition, decrease in the amount of forest cover is commonly associated with higher fragmentation (Ribeiro et al. 2009), with the creation of smaller and more isolated habitat remnants. In this scenario, it is also possible that gene flow among patches within these fragmented landscapes

was also negatively impacted, resulting in smaller effective population sizes and higher inbreeding.

Adults and seedlings can show distinct responses to anthropogenic disturbances (Van Geert et al. 2008). Due to time-lag effects it is expected that genetic diversity of adult perennial plants respond strongly to past landscape conditions rather than to recent habitat changes (Collevatti et al. 2001; Kramer et al. 2008). This is because changes in the composition and spatial configuration of landscapes occur faster than changes in the genetic diversity of arboreal plants, which can take many generations to respond genetically to human impacts (Landguth et al. 2010). Our results partially corroborate this hypothesis, as seedling and adults behave differently. Seedlings and adults inbreeding coefficients ( $f$ ) were both influenced by climate variation from the mid-Holocene to present-day. Adults  $H_e$  was also influenced by the same historical condition. Both seedling and adults showed to be negatively influenced by human impacts; however adults were mainly affected by the reduction of forest cover while seedling by the loss of large seed dispersers.

Climatic models forecast an increase in mean global temperature due to anthropogenic factors (IPCC 2007). Species can cope with global climate changes if their populations have the capacity to adapt to new environmental conditions or to disperse and track suitable habitats (Dawson et al. 2011). Unfortunately, most natural habitats have been replaced by anthropogenic landscapes dominated by agricultural fields and urban settlements (Foley et al. 2005), which may reduce the capacity of individuals to disperse and find suitable habitat. The amount of genetic diversity is essential for species to cope with environmental changes (Jump et al. 2009). Although *E. edulis* still has high genetic diversity, we showed that the spatial distribution of this species, as well as its genetic composition, is affected by climate changes. Therefore, an efficient species conservation planning should include the conservation of climatically stable areas that also harbors large extensions of forest and diversified animal community to preserve species interactions and ecological functions such as pollination and seed dispersal.

Finally, our results suggest that the pattern of genetic diversity in *E. edulis* is the outcome of historical instability during the mid-Holocene and current anthropogenic factors, mainly those that affect important ecological processes such as seed dispersal. Current human impacts may enhance historical processes, as well as shape the genetic diversity of heart of palm. Thus, an efficient plan for species conservation is urgent and must account for human impacts and environmental suitability, as well as assess genetic diversity of seedlings and adults in fragmented landscapes.

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**Author Contributions** C.S.Carvalho conceptualized and performed the study, analyzed the data and wrote the paper. M.C.Ribeiro, R.G.Collevatti and L. Ballesteros-Mejia participated in the study design, analyzed the data and contributed to writing the paper. M.C.Côrtes assisted in the data analyses and contributed to writing the paper. A.S.Santos contributed to the study conception and to writing the paper.

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