



Effects of defaunation of large seed dispersers, habitat loss and fragmentation on the population expansion of a tropical palm

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Abstract

Content Habitat loss and fragmentation are two processes resulting from land-use changes that significantly affect biodiversity worldwide. These two processes alongside illegal hunting are the main causes of the reduction in fauna diversity, richness, and biomass, which together characterize defaunation. Large animal species are the most affected by this process,

compromising ecosystem services such as seed dispersal.

Objectives We evaluated the isolated and combined effects of habitat loss, fragmentation and the nonrandom defaunation of large seed dispersers on the population expansions of the tropical palm *Euterpe edulis*.

Methods We modeled the spatial dynamics of the species via RangeShiftR in landscapes with different degrees of habitat percentage and fragmentation, simulating two distinct scenarios: nondefaunated, with a complete assembly of avian seed dispersers, and defaunated, with an impoverished assembly of large

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avian frugivores. Then, we developed linear regression models using the total abundance and density at the end of a 100-year simulation as response variable, and we selected the best model based on the Akaike information criterion.

Results Habitat loss, fragmentation, and defaunation negatively affect the abundance and density of *E. edulis*. Furthermore, the interaction effect between defaunation and habitat percentage was significant, indicating that in nondefaunated scenarios, the abundance and density of *E. edulis* increase substantially. Additionally, habitat loss has a greater negative effect on population expansion than fragmentation, which has a lower predictive power.

Conclusion These results help address the effects of habitat loss, fragmentation and defaunation on the population expansion of *E. edulis*. Our models contribute to the strategic planning of actions aimed at the conservation of *E. edulis*, highlighting habitat loss as a central point in allocating efforts for the protection of this species, as well as the importance of considering fauna data in estimates of the population expansion capacity of plant species.

Keywords Arecaceae · *Euterpe edulis* · Plant conservation · Atlantic forest · Population modeling · RangeShiftR

Introduction

The effects of anthropogenic activities over recent centuries have resulted in significant damage to biodiversity (Barnosky et al. 2012). This has led to the replacement of native habitats by human land use, reducing and fragmenting natural environments (Haddad et al. 2015; Rands et al. 2010). Habitat degradation coupled with hunting activities can result in a reduction in fauna diversity, richness, and biomass, a process known as defaunation (Dirzo et al. 2014; Redford 1992). The processes of habitat loss and fragmentation can intensify defaunation, as they result in a reduction in the quantity and quality of habitat and resources available for fauna, greater isolation of populations, and easier access for hunters (Fahrig 2003; Peres 2001; Tabarelli et al. 2004). Consequently, these processes can have cascading effects on the abundance and density of various plant species (Bomfim et al. 2018; Fahrig 2003) by directly

impacting ecosystem services, especially seed dispersal (Cardinale et al. 2012; Cordeiro et al. 2009; Emer et al. 2019; Herrmann et al. 2016; Wotton & Kelly 2011). Although numerous studies have indicated that habitat loss, fragmentation, and defaunation alter the dynamics of natural ecosystems and the perpetuation of species, few studies have evaluated the independent and synergistic effects of these processes.

Habitat loss and fragmentation are two processes resulting from land-use changes that significantly affect biodiversity worldwide (Haddad et al. 2015). Habitat loss, defined as the reduction in the total amount of available habitat, is widely recognized as a primary driver of population declines, as well as reduced genetic and species diversity (Fahrig 2003). The negative effect of habitat fragmentation, however, remains controversial (Fahrig 2017; Fahrig et al. 2019; Fletcher et al. 2018). By compiling several studies, Fahrig (2017) found that habitat fragmentation, when considered independent of habitat loss, often has weak effects on biodiversity, and when such effects occur, they are predominantly positive. These patterns remained consistent even when tropical and threatened species were analyzed separately. The positive effects of habitat fragmentation may occur because, for a given amount of habitat, a more fragmented landscape is composed of numerous small fragments with smaller distance between them, increasing the functional connectivity at landscape level (Fahrig 2017). Habitat fragmentation may also spread the risk of extinction over a larger number of sites, thereby reducing the likelihood of all local populations going extinct (Fahrig 2017). This, in turn, can have positive effects on several biodiversity parameters (Fahrig 2017). Although habitat loss and fragmentation usually happens simultaneously, understanding their individual and synergistic impacts provides a stronger scientific basis for conservation and management strategies.

Defaunation generally affects large animals disproportionately because they require larger living areas and more resources and are often the main targets of poaching (Dirzo et al. 2014; Young et al. 2016), compromising, for example, the role played by large seed dispersers (Harrison et al. 2013; Vidal et al. 2013). This can have negative effects on plants that rely exclusively or partially on these animals to disperse their seeds. Large seed dispersers have a greater capacity to cross extensive areas in fragmented

landscapes, transport more seeds, and disperse them to more diverse and distant locations from the mother plant (Donoso et al. 2017; Enquist et al. 2020; Jordano et al. 2007; Nathan et al. 2008; Pérez-Méndez et al. 2016). Forests where these large frugivores are absent suffer cascading damage in plant populations, as it collapses population expansion, reduces fruit removal success, and diminishes recruitment (Holbrook & Loiselle 2009; Markl et al. 2012; Pérez-Méndez et al. 2015, 2016).

The Atlantic Forest is one of the world's major biodiversity hotspots, with high rates of endemism and over 18,000 plant species, approximately 2.7% of which are endemic (Myers et al. 2000). However, the Atlantic Forest has experienced significant vegetation reduction, with only 23% of its original forest cover remaining, consisting of numerous small and discontinuous areas (Vancine et al. 2024). Among the plant species of the Atlantic Forest, the palm heart (*Euterpe edulis* Martius), which belongs to the Arecaceae family, stands out as one of the most important species for the maintenance of frugivorous fauna (Galetti & Aleixo 1998). This importance is due to its high fruit production, long annual fruiting periods, and significant variation in fruit size, thereby increasing the variety of animals that use the species as a food resource (Galetti & Aleixo 1998; Matos & Watkinson 1998; Reis 1995). Fruits and seeds of *E. edulis* can be consumed by 58 bird species and more than 20 mammal species (Galetti et al. 2013), making this food resource extremely important during times of scarcity of other fruits, mainly due to the lack of fruiting synchrony with other plants (Castro et al. 2007; García & Barbedo 2016). The strong attraction of animals, especially large vertebrates, to palm heart fruits can intensify gene flow between populations and accelerate colonization and restoration processes in natural environments, as these animals also disperse seeds of other species (Muler et al. 2014; Reis 1995).

The palm heart has a strong interdependent relationship with fauna. Its absence in forest remnants leads to the rapid reduction of medium- and large frugivorous vertebrates such as primates, toucans, and cracids (Silva & Tabarelli 2000; Galetti et al. 1997; Sodhi et al. 2004). On the other hand, the drastic reduction in large seed dispersers, particularly toucans, cotingas and guans, directly affects the quantity and quality of palm dispersal (Galetti et al. 2015) by reducing fruit removal and seed dispersal,

thus reducing seed migration to other populations (Galetti et al. 2013; Reis & Kageyama 2000; Rother et al. 2016; Sales et al. 2021). Small frugivores (e.g., thrushes) can ingest only smaller fruits and seeds and are unable to disperse the larger ones (Galetti et al. 2013). Smaller seeds cannot withstand long periods of desiccation and are less vigorous, which reduces their capacity to reach adulthood (Pizo et al. 2006; Sales et al. 2021). Additionally, smaller animals consume fewer seeds per visit but tend to visit the plant repeatedly, dispersing the seeds over shorter distances and often depositing them near or beneath the mother plant (Matos & Watkinson 1998; Pizo & Simão, 2001). This can impact genotypic diversity and the structure of the genetic pool, resulting in significant microevolutionary changes among populations (Carvalho et al. 2021, 2015, 2016; Galetti et al. 2013; Santos et al. 2016).

In addition to its great importance for local fauna, *E. edulis* also has high culinary and economic value, primarily because of its palm heart (apical meristem). However, harvesting palm hearts results in the death of the individual, preventing its regrowth. This uncontrolled exploitation intensifies the population decline and local extinctions observed in much of the remaining Atlantic Forest, leading the species to be classified as vulnerable on the Brazilian endangered species list (Reis & Kageyama 2000; Galetti & Fernandez 1998; Martinelli & Moraes 2013).

Given the invaluable role of *E. edulis* in maintaining various ecological processes and the current scenario of constant habitat loss, fragmentation and defaunation, it is urgent to predict how environmental changes may affect the ability of this palm to disperse through human-modified landscapes. In this context, the use of computational models that simulate different scenarios by incorporating multiple variables (species demographic data, dispersal estimates, stochastic events, landscape data, etc.) allows for the visualization and quantification of the influences of these variables on the organism's ability to disperse and colonize other environments (Huntley et al. 2010; Singer et al. 2016). These models can be excellent support tools for creating specific strategies for biodiversity conservation (Bocedi et al. 2014, 2021; Heikkinen et al. 2015). For example, the *RangeShiftR* package is a tool that enables the generation of spatially explicit, individual-based models that also include stochastic dynamics. Using data on

the demographic dynamics, dispersal, and landscape, this model can be used to understand eco-evolutionary dynamics and support species conservation. It is possible to model strategies for real populations in the short and long term by analyzing different scenarios, thereby providing options for management and understanding the range of reintroduced species (Bocedi et al. 2014; Malchow et al. 2021).

The aim of this study was to understand the effects of the habitat loss, fragmentation and defaunation of large seed dispersers on the population expansion of *E. edulis*. Here, population expansion was estimated as total abundance and density at the end of 100-year simulation. This understanding will help in the development of practices that aid in the conservation of this species, such as reintroduction and population reinforcement. To achieve this goal, we created landscapes with varying degrees of habitat percentage and fragmentation and constructed a population expansion model of *E. edulis*, considering demographic dynamics, dispersal, and the landscape. We hypothesize that habitat loss and defaunation have a greater impact on the population expansion of *E. edulis* compared to habitat fragmentation, leading to a reduction in the abundance and density of individuals. Habitat fragmentation will have a relatively minor effect on population expansion, because a more

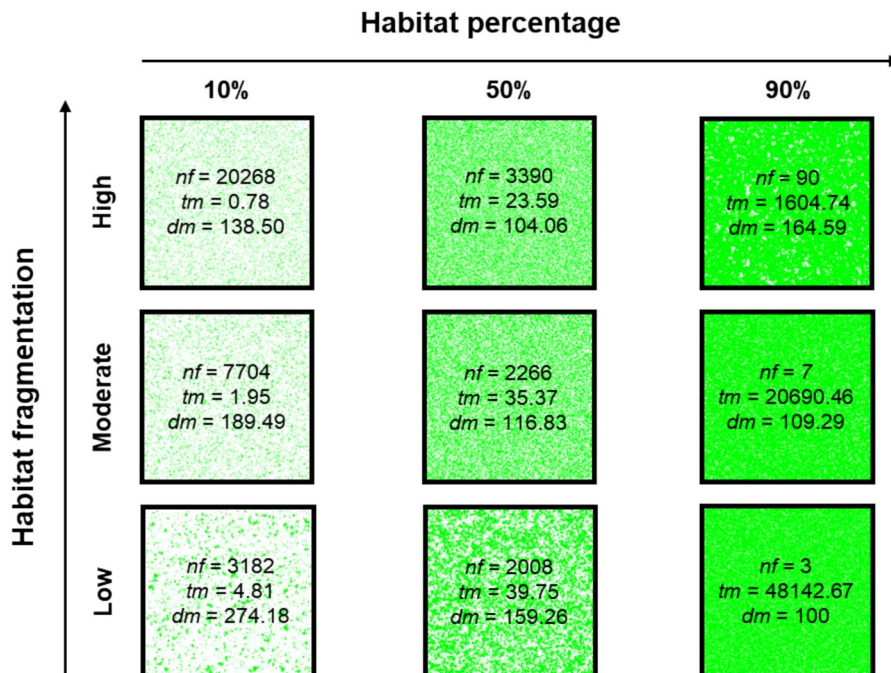
fragmented landscape typically consist of more fragments with smaller distance between them compared to a less fragmented landscape with the same amount of habitat.

Materials and methods

Simulated landscapes

To test the influence of the landscape structure on the population expansion of *E. edulis*, we simulated nine artificial landscapes with varying degrees of habitat percentage and fragmentation (Fig. 1). We used the *NLMR* package (Sciaini et al. 2018) in R software (version 3.5.2) to simulate neutral landscape models (NLMs). Specifically, we employed the modified random clusters (MRC) algorithm, derived from Saura & Martínez-Millán (2000), as it generates patterns that had better replicate the spatial heterogeneity observed in natural ecosystems. These patterns exhibit characteristics such as irregular patch shapes, varying sizes, and a range of spatial dependencies, which align with the dynamics of real landscapes influenced by ecological processes. The MRC method effectively mimics fragmentation gradients and patch aggregation levels

Fig. 1 Simulated landscapes with different habitat fragmentation (high, moderate and low) and habitat percentages, along with their respective number of fragments (*nf*), average fragment size (*tm*) in hectares and average distance between fragments (*dm*) in meters



observed in nature, making it suitable for modeling and analyzing ecological phenomena.

The artificial landscapes were generated in raster format, all with a resolution of 100 m, as required by the *RangeShiftR* package for dispersal kernel construction (see model elaboration section). The landscapes were 800×800 cells in size, consisting of binary habitat and nonhabitat values, where the habitat category simulated forest formations. To create different levels of habitat percentage and fragmentation, we used the parameter p (percolation probability), which represents the probability of a site being occupied by individuals (Saura & Martínez-Millán, 2000), and the parameter ai (proportion of randomly selected elements), which controls the landscape composition. Percolation probabilities (p) were set to high ($p=0.5$), moderate ($p=0.3$), and low ($p=0.1$) probability of a site being occupied. The proportion of randomly selected elements (ai) were set to 0.1, 0.5 and 0.9, generating landscapes with 10%, 50%, and 90% of habitat cover, respectively. To classify each landscape in terms of habitat fragmentation (high, moderate and low), we estimated the number of fragments (nf), the mean fragment size (tm) in hectares, the mean distance (dm) in meters between fragments, as shown in Fig. 1. Within landscapes with the same percentage of habitat, the greater the number of fragments, the smaller the fragment size and the shorter the mean distance; the higher the habitat fragmentation in that landscape. The mean fragment sizes ranged from 0.78 to 48,142.67 ha and the number of fragments from three to 20,268. Except for landscapes with 90% of habitat cover, those with higher habitat percentages and greater percolation probability had fewer but larger fragments. In contrast, lower habitat percentages and reduced percolation probability resulted in more numerous but smaller fragments (Fig. 1). In the case of landscapes with 90% habitat, higher values of percolation probability resulted in more fragmented landscapes. Distance metrics varied from 100 to 274.18 m, showing less pronounced variation among landscapes in average distance.

Model elaboration

To quantify the effects of large seed disperser defaunation, habitat loss and fragmentation on the population expansion dynamics of *E. edulis*, we used the *RangeShiftR* package available in R (Bocedi et al.

2021). Specifically, we created two scenarios: one representing defaunation of large avian seed dispersers (e.g. toucans, cotingas and guans), where only the seed dispersal distance of small avian frugivores, such as thrushes, was considered; and another representing a nondefaunation scenario, where the seed dispersal distance of both small and large avian frugivores were considered. To understand how habitat loss and fragmentation affect the expansion of *E. edulis* populations in defaunated and nondefaunated scenarios, we ran *RangeShiftR* via the simulated landscapes described above (see the Simulated landscape section). In the end, we obtained 18 models that encompassed all combinations of habitat percentage, fragmentation and defaunation status.

The *RangeShiftR* package operates by inputting parameters across several categories: I) landscape parameters; II) demographic parameters of the species under study; III) species dispersal parameters; IV) initialization parameters; and V) simulation parameters. Finally, all the parameters and data used for modeling are compiled and discussed below.

Landscape parameters

As described earlier, nine landscapes (Fig. 1) were simulated with varying degrees of habitat percentage and fragmentation. Each landscape consists of 800 columns and rows, with a resolution of 100×100 m and two landscape features (habitat and nonhabitat), totaling approximately 640,000 ha. Additionally, the demography density dependence in each habitat type (1/b), expressed in individuals per hectare, was determined using the *get localize* function and set as 30,000 (Supporting information—Figure S1).

Demographic parameters

We utilized a transition matrix derived from the matrix projection model to understand the population dynamics of *E. edulis*. In this model, the population is discretely analyzed (e.g., size classes, ontogenetic stages, or age classes), considering the structure over the sampling period. Thus, the transition matrix includes all probabilities of survival, regression, growth, and fecundity of individuals across the different classes (Caswell 2000).

For this study, we used the transition matrix of the species *E. edulis* (Souza et al. 2018) constructed

using temporal data collected in a preserved Montane Dense Ombrophilous Forest located in the state of Rio de Janeiro, Brazil. These data were gathered during three annual transition periods from 2012 to 2015. In 2012, all *E. edulis* individuals were marked with numbered tags and categorized into four ontogenetic stages: seedlings, preadult 1, preadult 2, and reproductive adults. Annual censuses were conducted for all stages to evaluate survival, growth, retrogression, reproductive status (inflorescence or fruit production), and fecundity (Souza et al. 2018). Additionally, newly recruited seedlings were tagged each year (Souza et al. 2018). This transition matrix was adjusted by adding a seed stage (Fig. 2) based on the

average number of seeds produced by a reproductive individual and its respective transition rate to the next stage of seedling (Silva & Reis 2019). Thus, the final transition matrix represents the average transition matrix calculated across the periods 2012–2013, 2013–2014 and 2014–2015, considering the five structured stages with overlapping generations.

The maximum age was set to 25 years according to various studies, including those conducted by Galetti et al. (2013) on *E. edulis*, as well as research involving other palm species, such as *Elaeis guineensis* Jacq. (Luskin & Potts 2011), which reported a maximum age of approximately 25 years. We subsequently determined the minimum ages for which

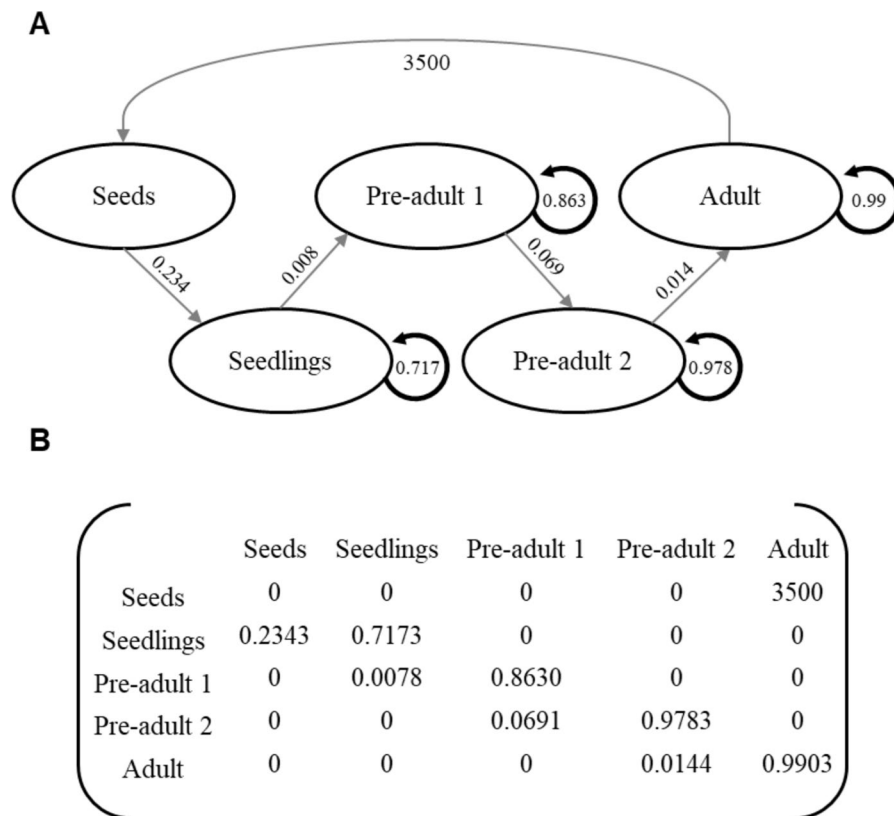


Fig. 2 **A** Life cycle diagram of the species *Euterpe edulis* based on data from Souza et al. (2018), with the addition of the seed stage (Silva & Reis 2019). Ellipses represent the five different growth stages, while arrows represent potential transitions between stages. Arrows originating and ending in the same stage represent stasis probabilities, whereas arrows connecting one stage to another represent growth probabilities. Specifically, the arrow linking the Adult stage to the Seeds stage does not represent a probability but rather an integer

value corresponding to the number of seeds a single adult individual can produce. **B** The average transition matrix calculated across the periods 2012–2013, 2013–2014 and 2014–2015 for the population of *Euterpe edulis* derived from its life cycle (A). The matrix elements represent the probability of survival and remaining in the same stage, the probability of survival and growth to the next stage, and the mean fecundity per reproductive individuals (the value of 3500)

an individual in stage $s-1$ must already have reached before it can develop into stage s as 0, 0, 4, 8, and 10 years for seeds, seedlings, pre-adult 1, pre-adult 2 and reproductive adults, respectively (Souza et al. 2018). We used the density dependence of individuals during the developmental phase, and survival was modeled to occur between reproductive events. For the type of reproduction, we chose the "asexual reproduction/female-only model" option, as it is the most suitable for species with monoecious mating systems.

Dispersal parameters

Dispersal was configured to vary according to the stages of individuals, with only individuals in stage 1 (seeds) considered capable of emigration. We set an emigration probability of 20% for the seeds based on the fruit dispersal rates reported by Reis & Kageyama (2000), a value also supported by Silva & Reis (2019). We applied the same emigration probability for defaunated and nondefaunated scenarios, as Carvalho et al. (2021) did not find differences in the number of *E. edulis* seeds dispersed in defaunated and nondefaunated forests.

Carvalho et al. (2021), on the other hand, found evidences of spatial dispersal limitation due to the loss of large avian frugivores, which can prevent seeds from reaching and colonizing new microhabitats, thereby intensify plant aggregation over time. Therefore, to simulate the nondefaunation and defaunation scenarios, we used the *DispersalKernel* function, which represents the statistical distribution of the probability of an individual moving a certain distance. Additionally, we utilized the *DoubleKernel* parameter within the *DispersalKernel* function, allowing us to include two sets of dispersal distances and their respective probabilities of occurrence. One dispersal kernel represented what is considered short-distance events for our focal species (100 m), which is expected in a defaunated scenario where only small frugivorous vertebrates, such as thrushes (*Turdus* spp.) remain. The other dispersal kernel represented long-distance events for our focal species (500 m) which is expected in a scenario where larger frugivores, such as cotingas *Procnias nudicollis*, toucans *Ramphastos* spp., and guans *Penelope* spp. and *Aburria jacutinga* persist. These values were obtained from Jordano et al. (2007), who documented the average seed dispersal distances for different frugivore

groups, and are supported by dispersal kernel estimates for seeds and pollen in a study by Santos et al. (2018) for *E. edulis* species.

Initialization parameters

During the initialization step, rules are defined for placing initial individuals on the landscape at the beginning of the simulation. We opted for free initiation based on the habitat map, starting with five different cells, thereby simulating five distinct populations in the landscape. We determined that all the habitat cells on the map were suitable for population initiation. The total number of initial individuals across all stages (excluding seeds) per hectare was set at 54,532, a quantity found in the studies by Souza et al. (2018). From this study, we also extracted data on the proportion of individuals in each ontogenetic stage (seeds, seedlings, preadult 1, preadult 2, and reproductive adults) within a 1-hectare area: 0, 0.866, 0.092, 0.036, and 0.006, respectively. The proportion of seeds was zero because the *RangeShiftR* platform does not allow populations to be initiated with individuals in the first stage. The density of reproductive adults for the initial condition was 327 (total number of reproductive adults [1635]/number of occupied cells [5]). Finally, the initial age distribution across the five ontogenetic stages was established based on minimum ages (0, 0, 4, 8, and 10 years).

Simulation parameters

The simulations were conducted with 20 replicates for each of the 18 scenarios, spanning 100 years each. Additionally, we specified in the model that individuals exceeding the boundaries of the landscape or reaching an invalid cell should be removed from the simulation. Furthermore, output files containing population abundance were generated every five years.

Statistical analysis

After running the model simulations, we used the abundance (total number of adult individuals in the landscape) and density of individuals (total number of adult individuals in the landscape divided by the number of habitat cells) after 100 years as dependent variables. Density was also included since abundance itself could be a mere consequence of the amount of

available habitat in the landscape. The independent variables included the habitat percentage, fragmentation degree, and defaunation status. We chose to use only abundance and density data for adult reproductive individuals, as they are most relevant for observing the expansion of established individuals in the population.

To identify which independent and combined variables (habitat percentage, fragmentation degree, and the presence or absence of large dispersers) best explained the abundance and density data of *E. edulis* after 100 years, we firstly assessed the most appropriate family distribution for each response variables using the *fitdist* function from *fitdistrplus* R package (Delignette-Muller & Dutang 2015). After applying a log-transformation to the raw data, the best-fit distributions for the response variables follow a Gaussian distribution (Fig S2–S7). Then, we fitted additive and interaction linear models. These models were compared via the model selection approach through the Akaike information criterion (AIC), which identifies the models that best explain the data. The models that presented the lowest AIC values were considered the best models (Burnham & Anderson 2002), with differences less than two AIC suggesting similar support between the models. The linear models were implemented in R software via the *lm* and *dredge* functions from the *MuMIn* package to automate model creation with all possible variable combinations, including a null model with a constant of 1. In total, nineteen models were generated for the abundance, and another nineteen were generated for the density of *E. edulis* as response variables. The *model.sel* function was subsequently employed to select models according to AIC, and the best models were then verified to ensure they met the assumptions of linear models (Fig. S8–S9). Then, we performed pairwise comparison among categories within predictors, using the *emmeans* function from the *emmeans* R package (Lenth 2025).

Results

We found that the abundance of *E. edulis* was best explained by the model that included all investigated variables, as well as the interactions between habitat percentage and defaunation, and between habitat percentage and fragmentation (Table 1). Additionally,

the null model, without any predictor variables, performed the worst among those tested. The regression coefficients for habitat percentage and defaunation status, as well as their interaction, were positive (Supporting information—Table S1) and all their pairwise comparisons were significant ($p < 0.001$, Table S2), indicating that the abundance of *E. edulis* increased in landscapes with greater habitat quantity and in scenarios without defaunation (Fig. 3, Table S2). Regarding habitat fragmentation, its negative effects on abundance were only evident in scenarios with lower habitat percentage (10% and 50%, Fig. 3, Table S2). In landscapes with 10% of habitat, greater fragmentation was associated with lower *E. edulis* abundance, with pairwise comparisons between fragmentation degrees being significant ($p < 0.001$, Table S2). In landscapes with 50%, the effects of habitat fragmentation were similar between moderate and high fragmentation ($p = 0.135$, Table S2, Fig. 3), but these effects were more negative compared to low fragmentation scenarios ($p < 0.001$, Table S2, Fig. 3). On the other hand, in landscapes with a high habitat amount (90%), abundance did not differ across varying degrees of habitat fragmentation (all p -values > 0.6 , Table S2, Fig. 3). Since habitat loss showed more consistent negative effects compared to habitat fragmentation, these results suggest that habitat quantity was more critical than the degree of fragmentation in this study.

The presence of fauna significantly contributed to increasing palm heart abundance (Fig. 3, Table S2), where in landscapes with high habitat percentages, the absence of large dispersers limited adult abundance in the landscape. For example, the abundance of adult palm heart individuals in the nondefaunated scenario with 50% habitat was greater than that in the defaunated scenario with 90% habitat (Fig. 3). Additionally, the abundance of *E. edulis* in the more preserved landscape (90% habitat percentage) was greater in the nondefaunated scenario than in the defaunated scenario (Fig. 3, Table S2).

The density of *E. edulis* was also better explained by the model with interactions between habitat percentage and defaunation, and between habitat percentage and fragmentation (Table 2 and Supporting Information—Table S3). Regarding habitat fragmentation, we found results similar to those observed for abundance when comparing its effects within each habitat percentage scenario (Fig. 3, Table S4). In

Table 1 Model selection for adult abundance of *Euterpe edulis* using Akaike Information Criteria

MODEL	AICc	Δ AIC	K	wAICc
FRAG + HBT + DEF + FRAG* HBT + HBT*DEF	− 266.70	0.00	13	0.73
FRAG + HBT + DEF + FRAG* HBT + FRAG* DEF + HBT*DEF	− 264.59	2.10	15	0.26
FRAG + HBT + DEF + FRAG* HBT + FRAG* DEF + HBT*DEF + HBT*PERC*DEF	− 257.79	8.90	19	0.00
FRAG + HBT + DEF + FRAG* HBT	− 57.53	209.17	11	0.00
FRAG + HBT + DEF + FRAG* HBT + FRAG* DEF	− 54.47	212.23	13	0.00
FRAG + HBT + DEF + HBT*DEF	74.60	341.30	9	0.00
FRAG + HBT + DEF + FRAG* DEF + HBT*DEF	78.00	344.69	11	0.00
FRAG + HBT + DEF	166.59	433.28	7	0.00
FRAG + HBT + DEF + HBT*DEF	170.13	436.83	9	0.00
HBT + DEF + HBT*DEF	253.11	519.80	7	0.00
HBT + DEF	309.87	576.57	5	0.00
FRAG + HBT + DEF + FRAG* HBT	547.08	813.78	10	0.00
FRAG + HBT	594.68	861.38	6	0.00
HBT	641.88	908.57	4	0.00
FRAG + DEF	866.26	1132.95	5	0.00
FRAG + DEF + FRAG*DEF	870.31	1137.01	7	0.00
DEF	887.07	1153.76	3	0.00
FRAG	965.80	1232.49	4	0.00
NULL MODEL	980.66	1247.36	2	0.00

All models include abundance as the response variable, and habitat percentage (HBT), habitat fragmentation (FRAG), and defaunation status (DEF) as predictor variables. *AICc* Akaike Information Criteria corrected for small sample sizes, Δ *AIC* difference in *AICc* value from the best model, *K* number of parameters, *wAICc* model weight of evidence relative to others

landscapes with 10% of habitat, greater fragmentation reduced *E. edulis* density ($p < 0.001$ for all pairwise comparison, Table S4). At 50% habitat, habitat fragmentation effects were similar between moderate and high fragmentation ($p = 0.153$, Table S4, Fig. 3), but more negative than low fragmentation scenarios ($p < 0.001$, Table S4, Fig. 3). In landscapes with 90% habitat, density was unaffected by habitat fragmentation (all p -values > 0.6 , Table S4, Fig. 3). However, overall, density was higher in landscapes with less habitat (Fig. 3), probably because fewer cells are occupied, which increases the density rapidly.

Overall, we found that defaunated landscapes have a lower adult palm heart density in comparison to nondefaunated landscapes, regardless of habitat percentage scenarios ($p < 0.001$, Fig. 3, Table S4). Specifically, in defaunated landscapes, the density was greater in areas with less habitat ($p < 0.001$, Table S4, Fig. 3), but similar between landscapes with 50% and 90% of habitat ($p = 0.67$, Table S4, Fig. 3), likely because dispersal constraints lead to propagule accumulation within the available area.

Discussion

Habitat loss, fragmentation and defaunation are often identified as the primary processes altering the dynamics of natural ecosystems and the perpetuation of species. However, their independent and synergistic effects remain poorly explored. In this study, we found that these processes interact synergistically to reduce the abundance and density of *Euterpe edulis*. Interestingly, defaunation exacerbated the negative impacts of habitat loss and fragmentation on *E. edulis* population, making these effects significantly more severe when compared to the threats occurring in isolation. This underscores the critical role of fauna in supporting the expansion of *E. edulis* populations. Our hypothesis that habitat loss and the extinction of large seed dispersers have a greater negative impact on the expansion of *E. edulis* populations than habitat fragmentation was also supported. Habitat loss consistently showed stronger negative effects than fragmentation in this study. However, when examining the density of palm tree individuals, our results

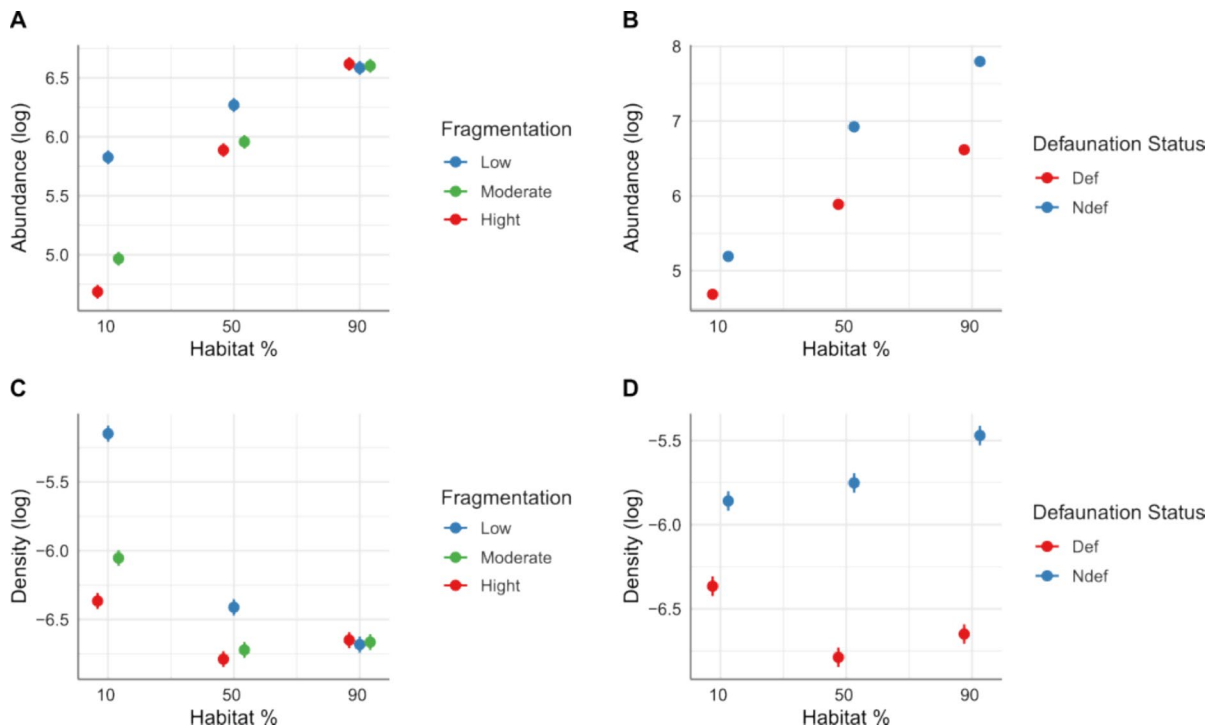


Fig. 3 Abundance (**A** and **B**) and density (**C** and **D**) of adult individuals of *Euterpe edulis* in the landscape relative to the three independent variables (percentage of habitat, habitat fragmentation, and defaunation status). *Def* Defaunated, *Ndef* Non-defaunated

differed slightly from those on abundance. Landscapes with less habitat exhibited higher density, likely because fewer occupied cells resulted in a rapid increase in density.

Compared with nondefaunated landscapes, defaunated landscapes presented a lower abundance and density of *E. edulis*, which aligns with various studies highlighting the importance of large frugivores for plant species that rely entirely or partially on these animals for dispersal. For example, Galetti et al. (2013) reported that areas with functional extinction of large frugivores are associated with reduced seed size, lower root biomass, and consequently reduced germination capacity and seedling survival (Leishman et al. 2000; Pizo et al. 2006). Furthermore, the loss of large dispersers hampers seed transport (Pérez-Méndez et al. 2016; Valverde et al. 2021) and can increase mortality rates due to seedling dependence on high density near the parent plant (Matos et al. 1999). Large dispersers, particularly avian dispersers, are also capable of crossing approximately five times longer distances than small and medium dispersers (Jordano et al. 2007; Vidal et al. 2013), which is

especially crucial in fragmented areas with significant distances between patches. The average isolation distance between forest patches in the Atlantic Forest is approximately 830 m (Vancine et al. 2024), a distance unlikely to be crossed by small dispersers, which typically have a dispersal range of less than 51 m from their source trees (Jordano et al. 2007). In our study, the average distance between fragments ranged from 100 to 275 m.

Overall, a greater abundance of *E. edulis* was observed in landscapes with greater habitat coverage. Studies conducted in Atlantic Forest environments, such as those by Emer et al. (2020), have revealed that both the number of plant species and the number of frugivorous bird species, along with their interactions, decrease as the habitat area decreases. Additionally, palm species, including *E. edulis*, have been reported to be highly susceptible to changes in habitat amount, with landscapes containing less than 40% forest cover supporting fewer than 10 of the 18 palm species studied (Benchimol et al. 2017). Specific investigations focusing on *E. edulis* have also identified the negative impact of habitat loss on its

Table 2 Model selection for adult density of *Euterpe edulis* using Akaike Information Criteria

MODEL	AICc	Δ AIC	K	wAICc
FRAG + HBT + DEF + FRAG* HBT + HBT*DEF	− 266.70	0.00	13	0.73
FRAG + HBT + DEF + FRAG* HBT + FRAG* DEF + HBT*DEF	− 264.59	2.10	15	0.26
FRAG + HBT + DEF + FRAG* HBT + FRAG* DEF + HBT*DEF + HBT*PERC*DEF	− 257.79	8.90	19	0.00
FRAG + HBT + DEF + FRAG* HBT	− 57.53	209.17	11	0.00
FRAG + HBT + DEF + FRAG* HBT + FRAG* DEF	− 54.47	212.23	13	0.00
FRAG + HBT + DEF + HBT*DEF	103.78	370.48	9	0.00
FRAG + HBT + DEF + FRAG* DEF + HBT*DEF	107.25	373.94	11	0.00
FRAG + HBT + DEF	189.13	455.83	7	0.00
FRAG + HBT + DEF + HBT*DEF	192.72	459.42	9	0.00
HBT + DEF + HBT*DEF	283.15	549.85	7	0.00
HBT + DEF	335.41	602.10	5	0.00
FRAG + DEF	349.15	615.85	5	0.00
FRAG + DEF + FRAG* DEF	352.92	619.61	7	0.00
DEF	447.37	714.07	3	0.00
FRAG + HBT + FRAG* HBT	547.08	813.78	10	0.00
FRAG + HBT	601.66	868.36	6	0.00
HBT	652.19	918.89	4	0.00
FRAG	657.92	924.62	4	0.00
NULL MODEL	700.58	967.28	2	0.00

All models include density as the response variable, and habitat percentage (HBT), habitat fragmentation (FRAG), and defaunation status (DEF) as predictor variables. *AICc* Akaike Information Criteria corrected for small sample sizes, Δ *AIC* difference in *AICc* value from the best model, *K* number of parameters, *wAICc* model weight of evidence relative to others

abundance. Indeed, the species has been locally extinct in all fragments within landscapes that are experiencing severe deforestation (<25% habitat) but has a relatively high abundance in landscapes with over 90% habitat (Leal et al. 2021, 2022).

In our models, the lower abundance of the species in landscapes with lower habitat percentages can be explained primarily by the species-area relationship, where larger areas provide greater support for species expansion, including a greater diversity of ecological interactions, habitats, and available resources, thereby hosting larger and more stable populations (Arrhenius 1921; Drakare et al. 2006; Rybicki & Hanski 2013; Watling et al. 2020; Wilson & Macarthur 1967). However, in natural environments, the lower abundance of the species in degraded landscapes may also be exacerbated by higher levels of illegal extraction. Degraded landscapes have become prime targets for illegal extractors (Tabarelli et al. 2004), as they have lower vegetation density (Crouzeilles et al. 2016), are predominantly outside protected areas (Gonçalves-Souza et al. 2021), have accessible trails

(Benítez-López et al. 2017), and are often near access infrastructures such as roads and highways (Laurance et al. 2014; Trombulak & Frissell 2000).

Our results also revealed that more connected landscapes with lower habitat amounts presented higher densities of heart palm individuals. Similar findings were reported in in situ studies, where higher densities of young *E. edulis* individuals were noted in the most fragmented areas (Baggio et al. 2023). This outcome was attributed to reduced intra- and interspecific competition in the more fragmented area (Baggio et al. 2023). In contrast, Melito et al. (2014) reported divergent results, observing that fragments with smaller habitat extents presented lower individual densities across all life stages. Additionally, studies indicate that *E. edulis* density may not vary significantly with the fragment size (Portela & Santos, 2014). Our results can be explained primarily by the structure and composition of the simulated landscapes. The simulated landscapes with limited habitat and high fragmentation had an average distance of 138 m between fragments. Given that the average

seed dispersal distance was 100 m in the defaunated scenarios and 500 m in the nondefaunated scenarios, the average distance in our simulated landscapes did not hinder functional connectivity between fragments. Since landscapes with low habitat (10%) had few areas to be occupied but were functionally connected, this led to a significant increase in the *E. edulis* density.

Fragmentation alone was the variable that showed the weakest predictive power for the *E. edulis* abundance and density data in our study. Other recent studies have found similar results (Fahrig 2017; Fahrig et al. 2019; Fletcher et al. 2018), with fragmentation itself, isolated from habitat loss, showing no significant influence (Fahrig 2003) or even positive effect on plant species abundance and richness (Fahrig 2017). One possible explanation for the limited influence of fragmentation alone in our analyses lies in the concept of increased functional connectivity (Fahrig 2017; Goodwin 2003; Goodwin & Fahrig 2002). Increased fragmentation creates more numerous and smaller patches with shorter distances between them, potentially increasing the likelihood that dispersing organisms encounter a patch (Fahrig 2017; Fahrig et al. 2019). A similar situation was found in our results: when we generated simulated landscapes with fixed habitat percentages and varied only the degree of percolation, we ultimately divided the area into different patches but did not significantly alter the average distances between the patches (the average distance between patches ranged from 100 to 275 m, Fig. 1). In this context, we should not disregard the effects of fragmentation on biodiversity; however, it is essential to consider the habitat percentage, which can influence the distances between patches (Edelsparre et al. 2018; Hanski 1998).

Finally, our results contribute significantly to advancing research on the synergistic and separate effects of habitat loss, fragmentation, and defaunation on plant populations, a highly complex theme with considerable challenges in situ (Fahrig 2017; Mancini et al. 2023; Püttker et al. 2020). The methodology adopted proved robust and effective in recreating natural relationships and the underlying complexities of these processes. Most tree species in tropical forests are animal dispersed (Jordano, 2007) and defaunation of large frugivores is becoming pervasive in fragmented and non-fragmented forests. Thus, our results have significance for many other species similar to *E.*

edulis population dynamics. However, we emphasize the pressing need for more empirical research on seed dispersal distance in tropical ecosystems to obtain more specific and reliable parameters for the model. Similarly, studies aiming to understand the differences in the demographic dynamics between fragmented versus preserved landscapes are crucial, given that in this study, we assumed that the demographics of a population in a fragmented area were equivalent to those in a well-conserved area (Silva & Reis 2019; Souza et al. 2018). With respect to landscape characteristics, future research should focus on generating landscapes with continuous values for habitat percentage and fragmentation to identify thresholds beyond which habitat quantity significantly affects plant abundance and density. Creating landscapes with habitat fragmentation variation will allow for more representative assessments of distances between fragments, as well as investigations of a potential fragmentation threshold where habitat loss becomes dependent on fragmentation (Andrén & Andrén 1994; Fahrig 1997; Swift & Hannon 2010).

Conclusion

Our results help clarify the independent and synergistic effects of anthropogenic processes affecting various species worldwide. Synergistically, habitat loss, fragmentation, and defaunation of large frugivores are the factors that most strongly limit the abundance and density of *E. edulis*. Moreover, habitat loss was an important factor negatively affecting *E. edulis* abundance, highlighting its critical role as a central focus for conservation efforts. This is particularly relevant in the Atlantic Forest, where only a small percentage of the original habitat remains. Additionally, the interaction models were significant between defaunation and habitat percentage, indicating that in the nondefaunation scenarios, the abundance substantially increased in areas with high habitat percentages. Therefore, our results emphasize the importance of projects aimed at restoring populations of plant species, including measures for rewilding, as proposed by Oliveira-Santos & Fernandez (2010). With the restoration of native fauna, the management of a fauna-dependent species can be accelerated, restoring previously lost ecosystem services such as dispersal (Carvalho et al. 2021; Fernandez et al. 2017).

Finally, fragmentation per se was the variable that had the least influence on population expansion and abundance, highlighting how habitat quantity is more crucial than the degree of fragmentation in this study.

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Data availability The authors confirm that the data supporting the findings of this study are available within the article its supplementary materials.

Declarations

Conflict of interest All authors declare that they have no conflicts of interest.

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