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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 degradation and hunting are the main causes of the reduction in fauna diversity, richness, and biomass, characterizing defaunation. Large animal species are the most affected by this process, compromising ecosystem services such as seed dispersal.

Objectives

We evaluated the effects of the nonrandomdefaunation of large seed dispersers, habitat loss and fragmentation on the expansion dynamics of tropical palms (*Euterpe edulis*) populations.

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 seed dispersers, and defaunated, with an impoverished assembly of large frugivores. Then, we developed linear regression models, and the best model was selected using the Akaike information criterion.

Results

Habitat loss, fragmentation, and defaunation synergistically affect the abundance and density of palm hearts. Furthermore, the interaction effect between defaunation and habitat percentage was significant, indicating that in nondefaunation scenarios, the abundance and occupation of palm hearts increase substantially. Additionally, habitat loss has a greater effect on population expansion than fragmentation, which has a lower predictive power.

Conclusion

These results help addressthe individual and synergistic effects of defaunation, habitat loss and fragmentation on the population expansion of palm hearts. Our models contribute to the strategic planning of actions aimed at the conservation of palm hearts, 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.

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 (de Assis 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.

Defaunation generally affects large animals disproportionately because these animals require larger living areas and more resources and are often the main targets of illegal hunting (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; Garcia & 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 drastic reduction in large seed dispersers, particularly birds and mammals, 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 larger seeds (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 and tend to disperse them over shorter distances, 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) and as threatened according to the International Union for Conservation of Nature (IUCN) Red List (de Lima et al., 2024). Consequently, the absence of this species in forest remnants leads to the rapid reduction of medium- and large frugivorous vertebrates such as primates, toucans, and cracids (da Silva & Tabarelli, 2000; Galetti et al., 1997; Sodhi et al., 2004).

Given the invaluable role of *E. edulis* in maintaining various ecological processes and the current scenario of constant defaunation, habitat loss, and fragmentation, 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 dynamics of *E. edulis*. 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 loss and fragmentation and constructed a population expansion model of palm hearts, considering demographic dynamics, dispersal, and the landscape. We hypothesize that habitat loss and defaunation have a more significant impact on the population expansion of *E. edulis*, resulting in a reduction in the

abundance and density of individuals. We hypothesize that fragmentation will have a comparatively smaller impact on population expansion, as it creates areas with breaks but does not result in significant distances between patches when habitat loss is not concurrent.

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 loss 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 algorithm, derived from Saura & Martínez-Millán (2000)'s study, as it produces results more similar to natural fragmentation patterns and allows independent analysis of fragmentation and habitat loss.

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 fragmentation, we used the parameter *p* (percolation probability), which represents the probability of a site being occupied by individuals (Saura & Martínez-Millán, 2000), and habitat loss was simulated via the parameter *ai* (proportion of randomly selected elements), which controls the landscape composition. Percolation probabilities were set to slightly fragmented (*p=0.5*), moderately fragmented (*p=0.3*), and highly fragmented (*p=0.1*), and habitat percentages varied at 10% (*ai=0.1*),50% (*ai=0.5*), and 90% (*ai=0.9*). For each landscape, we estimated the mean fragment size (*tm*) in hectares and the mean distance (*dm*) in meters between fragments, as shown in Fig. 1. The mean fragment sizes ranged from 0.78 to 48,142.67 ha; landscapes with more habitat and less fragmentation had larger fragments, whereas lower habitat percentages and greater fragmentation led to smaller fragments. 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 seed dispersers, where only the seed dispersal distance of small frugivores was considered, and another representing a nondefaunation scenario, where both small and large seed dispersal distances 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 defaunation status, habitat loss, and fragmentation.

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 maximum value of 30,000 individuals/hectare was determined using the *get localize* function for the strength of density dependence (1/b), an important parameter that directly affects population equilibrium size and maximum abundance (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) on the basis of temporal data collected in a preserved Montane Dense Ombrophilous Forest located in the state of Rio de Janeiro, Brazil. This matrix was adjusted by adding a seed stage (Fig. 2) on the basis of 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, we determined that the population would consist of five structured stages with overlapping generations. These stages were delineated based on the ontogenetic development of individuals, with the 1^{st} stage being seeds, the 2^{nd} stage being seedlings, the 3^{rd} stage being preadult 1, the 4^{th} stage being preadult 2, and the 5^{th} stage being reproductive adults, similar to field studies (Portela & Santos, 2011)

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 ages for transition between each stage as 0, 4, 8, and 10 years. 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 option "asexual reproduction/female-only model", as recommended by the creators of the *RangeShiftR* platform, given the absence of specific parameters for plant species.

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 according to the fruit dispersal rates of Reis & Kageyama (2000), a value also supported by Silva & Reis (2019).

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 short-distance events (expected in a defaunated scenario where only small frugivorous vertebrates remain), whereas the other represented long-distance events (expected in a scenario where larger vertebrates persist). Thus, we determined the values for short-distance dispersal as 100 m and for long-distance dispersal as 500 m, each with a probability of occurrence of 50%. 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 on the basis of 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). For 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. Finally, the initial age distribution across the five ontogenetic stages was established on the basis of 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 and occupancy data 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. The independent variables included the habitat percentage, fragmentation degree (percolation), and defaunation. 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. Additionally, the normality of the abundance and density data of *E. edulis* after 100 years was assessed via the Shapiro–Wilk normality test, which was conducted in R.

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 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 are considered the best models (Burnham & Anderson, 2002), with differences less than two 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 on the basis of the AIC.

Results

We found that the abundance of *E. edulis* was best explained by the full model, which included all investigated variables and their possible interactions (Table 1). Additionally, the null model, without any predictor variables, performed the worst among those tested. The regression coefficients for all the variables were positive (Supporting information - Table S1), indicating that the abundance of *E. edulis* increased in landscapes with greater habitat quantity, greater percolation, and scenarios without defaunation (Fig. 3). Percolation was the least influential factor, especially in landscapes with high habitat percentages, highlighting that habitat quantity was more critical than the fragmentation degree in this study (Fig. 3).

The presence of fauna significantly contributed to increasing palm heart abundance, where in landscapes with high habitat percentages and high percolation, 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. Additionally, the abundance of *E. edulis* in the more preserved landscape (0.5% percolation and 90% habitat percentage) was 3.5 times greater in the nondefaunated scenario than in the defaunated scenario.

Table 1. Model selection for adult abundance of *Euterpe edulis* using Akaike Information Criteria. All models include abundance as the response variable, and habitat percentage (HBT), fragmentation (represented by percolation: PERC), and defaunation (DEF) as predictor variables. AICc: Akaike

Information Criteria corrected for small sample sizes; ΔAIC: difference in AICc value from the best model; K: number of parameters; wAICc: model weight of evidence relative to others.

MODEL	AICc	ΔAIC	K	wAICc
HBT + PERC + DEF + HBT*PERC + HBT*DEF + PERC*DEF + HBT*PERC*DEF	4331.7	0.00	19	0.86
HBT + PERC + DEF + HBT*PERC + HBT*DEF + PERC*DEF	4335.4	3.66	15	0.14
HBT + PERC + DEF + HBT*PERC	4362.6	30.85	13	0.00
HBT + PERC + DEF + HBT*DEF + PERC*DEF	4433.9	102.16	11	0.00
HBT + PERC + DEF + HBT*DEF	4453.3	121.59	9	0.00
HBT + DEF + HBT*DEF	4643.4	311.69	7	0.00
HBT + PERC + DEF + HBT*PERC	5218.7	886.94	11	0.00
HBT + PERC + DEF + HBT*PERC + PERC*DEF	5220.2	888.46	13	0.00
HBT + PERC + DEF	5220.5	888.82	7	0.00
HBT + PERC + DEF + PERC*DEF	5222.0	890.32	9	0.00
HBT + DEF	5245.4	913.69	5	0.00
HBT + PERC	5566.4	1234.72	6	0.00
HBT + PERC + HBT*PERC	5570.9	1239.22	10	0.00
HBT	5573.6	1241.91	4	0.00
PERC + DEF	5672.0	1340.32	5	0.00
PERC + DEF + PERC*DEF	5675.4	1343.71	7	0.00
DEF	5676.4	1344.64	3	0.00
PERC	5806.1	1474.36	4	0.00
NULL MODEL	5807.8	1476.08	2	0.00

Since the abundance values correspond to the total abundance in the landscape, this result could be a consequence of the amount of available habitat. Therefore, we also analyzed the density of adult individuals in the landscape by dividing their abundance by the number of available habitat cells. The density of *E. edulis* was also better explained by the model with interactions involving habitat loss, fragmentation, and defaunation (Table 2 and Supporting Information - Table S2). Overall, we found that defaunated landscapes have a lower adult palm heart density. Specifically, in defaunated landscapes, the density was consistently greater in areas with less habitat and greater percolation (Fig. 4), likely because dispersal constraints lead to propagule accumulation within the available area. In nondefaunated

landscapes, the density was greater in landscapes with less habitat and greater percolation, probably because fewer cells are occupied, which increases the density rapidly.

Table 2. Model selection for adult density of *Euterpe edulis* using Akaike Information Criteria. All models include density as the response variable, and habitat percentage (HBT), fragmentation (represented by percolation: PERC), and defaunation (DEF) as predictor variables. AICc: Akaike Information Criteria corrected for small sample sizes; ΔAIC: difference in AICc value from the best model; K: number of parameters; wAICc: model weight of evidence relative to others.

MODEL	AICc	ΔAIC	K	wAICc
HBT + PERC + DEF + HBT*PERC + HBT*DEF + PERC*DEF + HBT*PERC*DEF	-4101.2	0.00	19	1.00
HBT + PERC + DEF + HBT*PERC + HBT*DEF + PERC*DEF	-4079.7	21.46	15	0.00
HBT + PERC + DEF + HBT*PERC + PERC*DEF	-4072.4	28.82	13	0.00
HBT + PERC + DEF + HBT*PERC + HBT*DEF	-4054.0	47.17	13	0.00
HBT + PERC + DEF + HBT*PERC	-4047.5	53.66	11	0.00
HBT + PERC + DEF + HBT*DEF + PERC*DEF	-3723.6	377.65	11	0.00
HBT + PERC + DEF + PERC*DEF	-3723.5	377.70	9	0.00
HBT + PERC + DEF	-3716.6	384.57	7	0.00
HBT + PERC + DEF + HBT*DEF	-3716.6	384.61	9	0.00
HBT + PERC + HBT*PERC	-3637.8	463.40	10	0.00
PERC + DEF + PERC*DEF	-3598.0	503.24	7	0.00
PERC + DEF	-3594.4	506.85	5	0.00
HBT + DEF	-3574.1	527.08	5	0.00
HBT + DEF + HBT*DEF	-3572.7	528.47	7	0.00
HBT + PERC	-3500.5	600.74	6	0.00
DEF	-3489.4	611.84	3	0.00
PERC	-3430.2	670.99	4	0.00
HBT	-3417.3	683.87	4	0.00
NULL MODEL	-3361.8	739.40	2	0.00

Discussion

Our hypothesis that habitat loss and the extinction of large seed dispersers would more significantly affect the expansion of *E. edulis* populations was corroborated. Our results demonstrated that the model that best explained the palm heart abundance over the 100-year simulation included all the variables (habitat loss, fragmentation, and defaunation) and their possible interactions. The models revealed that habitat loss is more critical than fragmentation in ensuring a high abundance of *E. edulis*. When considering the density of palm tree individuals, our results differed somewhat from that of abundance, as higher percolation favored higher density in landscapes with little habitat, likely because fewer cells were occupied, which rapidly increased the density. Additionally, our results highlighted the importance of fauna in the expansion of *E. edulis* populations. In defaunated scenarios with high habitat availability, the abundance was significantly lower than that in a nondefaunated scenario with 50% habitat.

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 (Silva 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).

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 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). In terms of empirical data, 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 & dos Santos, 2014). Our results can be explained primarily by the structure and composition of the simulated landscapes. The simulated landscapes with limited habitat and low percolation 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. This finding is closely tied to recent discussions (Fahrig, 2017; Fahrig et al., 2019; Fletcher et al., 2018), where it has been noted that most studies isolating fragmentation from habitat loss do not find significant effects (Fahrig, 2003) or positive effects, such as increasing species richness and abundance (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 landscapes ranged from 64 to 135 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. However, we emphasize the pressing need for more empirical research on *E. edulis* to obtain more specific and reliable parameters for the model. For example, the scarcity of studies investigating dispersal distances across a wide range of seed dispersers for this species is alarming. Similarly, studies aiming to understand the differences in the demographic dynamics of *E. edulis* in 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 percolation probability to identify thresholds beyond which habitat quantity significantly affects *E. edulis* abundance and density. Creating landscapes with greater percolation 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 & Andren, 1994; Fahrig, 1997; Swift & Hannon, 2010). Nevertheless, despite these limitations, our results are largely consistent with the literature for this species.

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, as an independent variable, habitat loss provided the strongest support for explaining abundance, making habitat loss a central point for allocating efforts to protect biodiversity, especially in the Atlantic Forest, where only tiny percentages of the original areas remain. 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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Figures

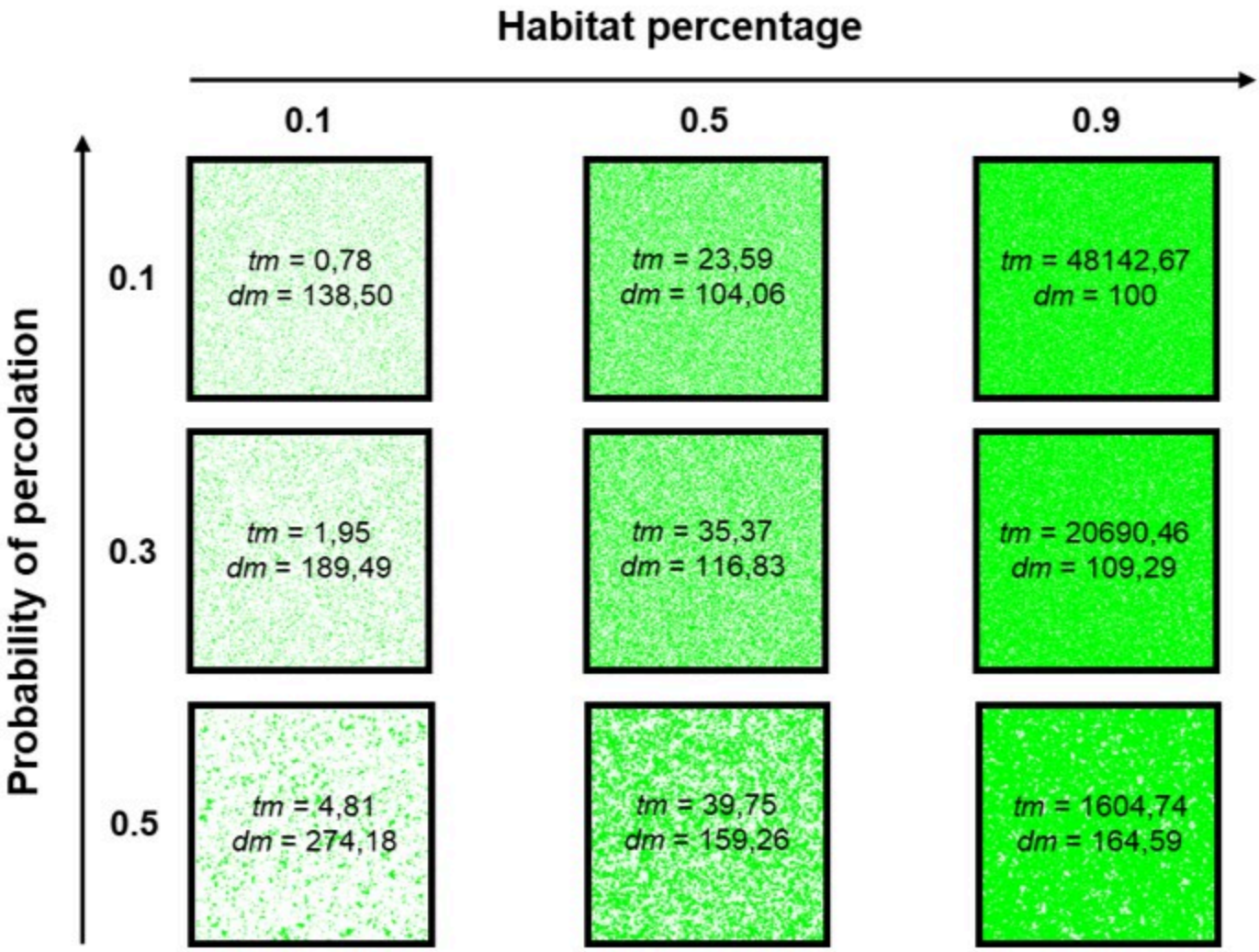

Figure 1

Simulated landscapes with different percolation probabilities (*p*) and habitat percentages (*ai*), along with their respective average fragment size (*tm*) in hectares and average distance between fragments (*dm*) in meters.

	Seeds	Seedlings	Pre-adult 1	Pre-adult 2	Adult
Seeds	0	0	0	0	3500
Seedlings	0.2343	0.7173	0	0	0
Pre-adult 1	0	0.0078	0.8630	0	0
Pre-adult 2	0	0	0.0691	0.9783	0
Adult	0	0	0	0.0144	0.9903

Figure 2

Transition matrix for the population of *Euterpe edulis* based on data from Souza; Portela; Mattos (2018), with the addition of the seed stage (Silva & Reis, 2019). The matrix was developed based on vital rates of survival and transition between the following ontogenetic stages of the species: 1st Seeds, 2nd Seedlings, 3rd Pre-adult 1, 4th Pre-adult 2, and 5th reproductive Adults, represented by rows and columns.

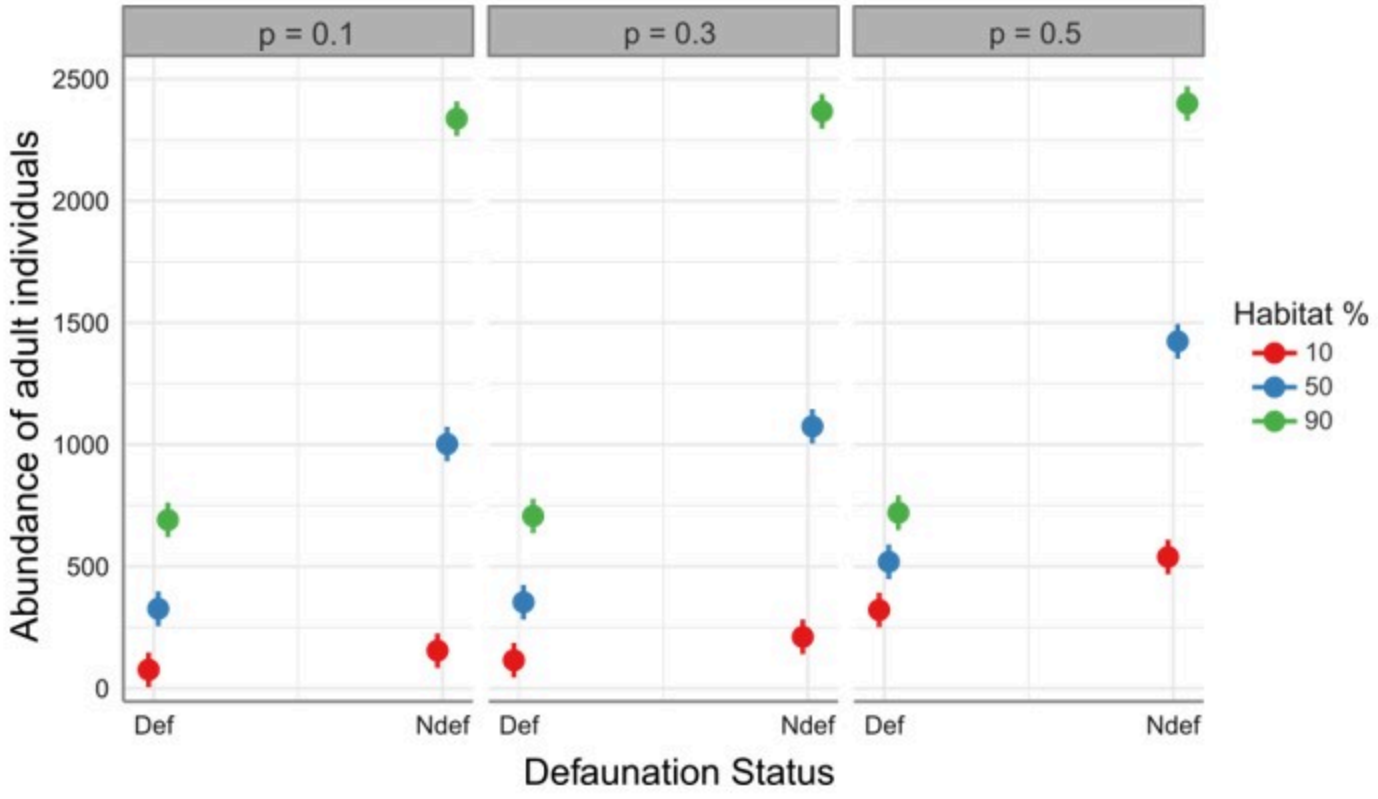

Figure 3

Abundance of adult individuals in the landscape relative to the three independent variables (percentage of habitat, percolation, and defaunation status). Lower percolation values (shown at the top of the graphs) indicate more fragmented landscapes. Def: Defaunated; Ndef: Non-defaunated; p: percolation probability.

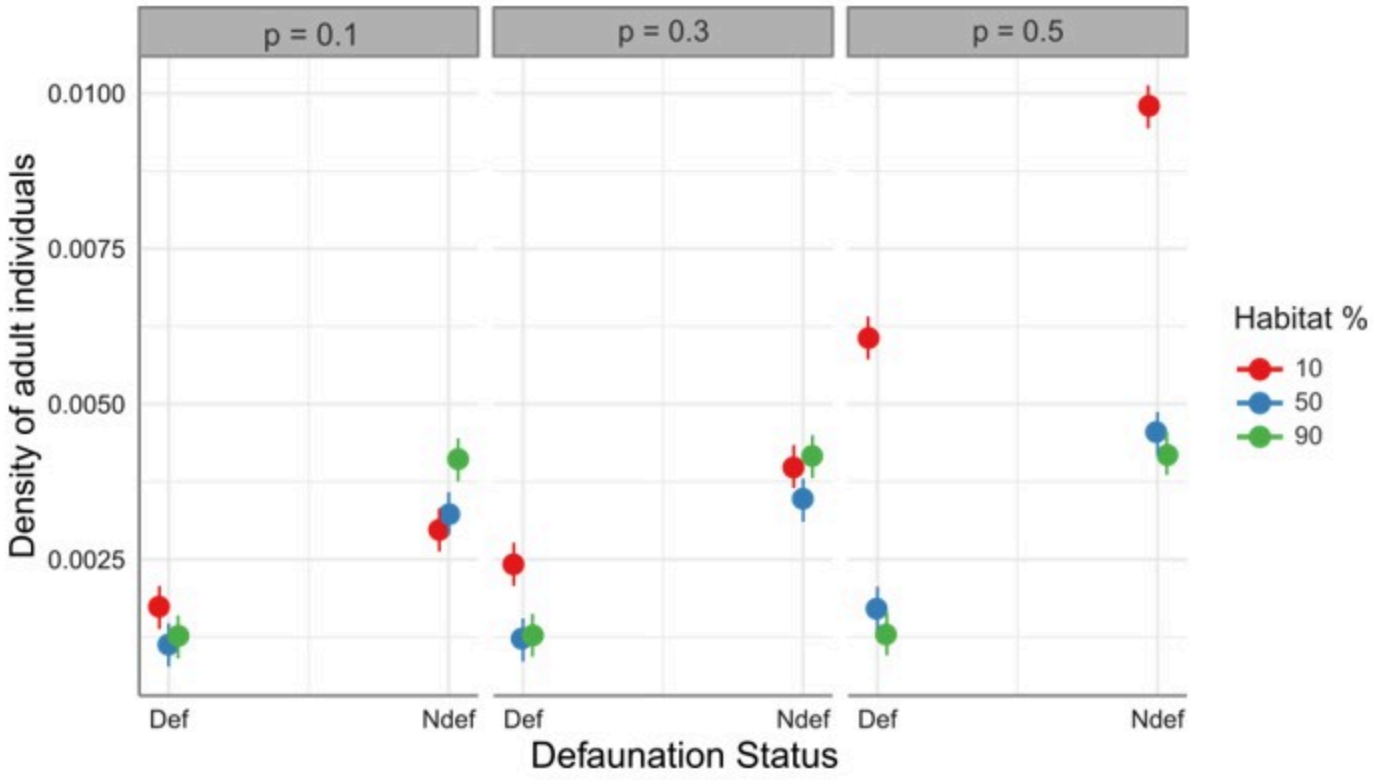

Figure 4

Adult density in relation to the three independent variables (percentage of habitat, percolation, and defaunation status). Lower percolation values (shown at the top of the graph) indicate more fragmented landscapes. Def: Defaunated; Ndef: Non-defaunated; p: percolation probability.

Supplementary Files

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