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ORIGINAL ARTICLE

Large herbivores regulate the spatial recruitment of a hyperdominant Neotropical palm

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Abstract

Large mammalian herbivores play an important role in shaping the diversity of tropical forests by affecting the survival of seedlings and saplings beneath parent plants. The white-lipped peccary (*Tayassu pecari*) accounts for the largest herbivore biomass that controls seed and seedling survival in Neotropical ecosystems. However, hunting and habitat loss has driven peccaries to local extinction for most of their original distribution, so it is likely that their absence will affect plant recruitment dynamics. We tested the effects of peccary local extinction on the density and spatial distribution of the hyperdominant palm *Euterpe edulis* by performing a fine-scale characterization of its spatial recruitment in six forest sites in the Brazilian Atlantic forest. We compared the age structure and the spatial patterns of seedlings, saplings, and adults as well as the relationship between them. We found that while under the presence of peccaries there was a decrease in recruitment rates under adults, the local extinction of these large mammals led to a more clumped process of spatial recruitment. Despite such contrasting spatial patterns of recruitment dynamics, neither age structure nor the random spatial distribution of adults was affected by the presence or absence of peccaries, indicating that their early effects on these palm populations are mitigated as recruitment advances. Our findings highlight the role of large-bodied forest-dwelling herbivores in regulating the fine-scale spatial recruitment of plants and advance our understanding on the effects of defaunation in tropical forests.

Abstract in Portuguese is available with online material.

KEYWORDS
Atlantic forest, defaunation, *Euterpe edulis*, plant recruitment, seed predation

1 | INTRODUCTION

Defaunation, local, global, or functional loss of animals, is becoming a ubiquitous component of tropical ecosystems (Benítez-López et al., 2019; Dirzo et al., 2014). One of the most affected animal groups are large mammalian herbivores (Dirzo et al., 2014; Jorge et al., 2013; Ripple et al., 2015) that play an important role in the regulation of plant populations through seed dispersal and predation, herbivory, and trampling of seedlings (Kurten & Carson, 2015; Villar et al., 2020). The non-random foraging of large herbivores can affect spatial recruitment patterns of plant species, which in turn affects plant communities in these ecosystems (Asquith et al., 1997; Connell, 1971; Janzen, 1970). Therefore, their local extinction could cause a cascade of effects which may, over time, alter the structure of these ecosystems. Understanding the spatial processes of plant recruitment derived from these extinctions in local populations is crucial for the development of integrated conservation plans that take this type of interaction into account.

The white-lipped peccary (*Tayassu pecari*; WLP, hereafter), a forest-dwelling 30 kg ungulate, comprises the largest herbivore biomass in pristine Neotropical ecosystems (Peres, 1996). In areas without significant hunting pressure, the WLP represents the largest mammalian biomass (e.g., up to 370 kg/km^2; Peres, 1996). Because this species forages in large herds (>50 individuals), consuming fruits, seeds, and seedlings (Beck, 2006), WLP is an important regulator of the recruitment of many plant species (Beck, 2005; Keuroghlian & Eaton, 2009; Villar et al., 2020). However, WLP is a primary target for hunters and has become locally extinct in most of its distribution (Altrichter et al., 2012; Thornton et al., 2020). Consequently, the population dynamics of some of the plant species consumed by this ungulate may have been altered (Silman et al., 2003).

In the Atlantic rainforest, among the resources mostly consumed by WLP are the seeds and seedlings of the palm *Euterpe edulis* (Arecaceae) (Akkawi et al., 2020; Keuroghlian & Eaton, 2009), considered to be a key species in this ecosystem. Its fruits constitute an important resource for frugivores due to the dominance of this species over other tree species (Benchimol et al., 2017), for its bearing of fruit in times of fruit shortage (Castro et al., 2007; Staggemeier et al., 2016), and its lipid-rich fruits (Galetti et al., 2013). Despite its importance, palm-heart harvesting and defaunation have negatively impacted this species (Galetti & Fernandez, 1998). For example, it has been documented that habitat fragmentation (Carvalho et al., 2015; Santos et al., 2016) and defaunation of large seed dispersers (Carvalho et al., 2016; Galetti et al., 2013) led to changes in seed size with potential consequences for plant demography. The loss of large herbivores results in a turnover of the guild of seed and seedling predators, with an increase of early stages mortality mainly due to agouti and small rodents (Fadini et al., 2009; Galetti et al., 2015). The amount of information about *E. edulis* has made this species a reference in the study of the ecological and evolutionary effects of habitat loss and defaunation in this ecosystem; however, there are still some gaps of knowledge in the literature. For example, despite the importance of density-dependent mortality as a population-thinning agent (Zhou & Chen, 2010), previous studies have not addressed the consequences that the disappearance of the main predator of seeds and seedlings has on the spatial recruitment patterns of this species.

In most tropical plants, density-dependent mortality in the early ontogenetic stages may modulate the recruitment patterns in such a way that the probability of survival increases with distance from mass seed dispersal sites (Connell, 1971; Janzen, 1970). Since the highest density of dispersed seeds is usually located under the mother plant, the recruitment dynamics expected under this effect would imply a progressive trend toward spatial segregation between individuals. In this regards, because peccaries are the major agents of seed and seedling mortality in *E. edulis*, their disappearance is expected to counteract the survival probability predicted by the Janzen–Connell hypothesis. Although this effect has been described for some tropical palm species (e.g., *Astrocaryum murumuru*; Silman et al., 2003), its strength may vary among species even within the same ecosystem due to additional compensatory mechanisms (Comita et al., 2014; Hammond & Brown, 1998). In *E. edulis*, the effect of the loss of the main seed predator on the spatial dynamics of recruitment remains unexplored. Addressing this issue in a dominant species that is key to the Atlantic Forest offers a unique opportunity to explore the effects of defaunation in an ecosystem that is highly diverse.

Here, we tested the consequences of the local extinction of WLP on the demography and spatial distribution of *E. edulis*. We use fine-scale spatial analysis of the spatial pattern of seedlings, saplings, and adults and the relationship between them and compare these patterns between forests were WLP is present and forests were WLP is absent. Our two hypotheses are that the local extinction of peccaries would (a) increase the recruitment in this palm species and therefore alter its age structure; and (b) release early ontogenetic stages from part of the negative density-dependent effects, thus modifying the spatial dynamics of recruitment.

2 | MATERIALS AND METHODS

2.1 | Study areas

During 2008 and 2010, we established 11 plots in 6 sites along the Atlantic forest of Brazil with contrasting abundance of WLP (Figure 1a). We chose the sampling areas based on previous mammal censuses and literature, so that we had enough certainty of the presence or absence of WLP (Galetti et al., 2017; Table S1).

We set up five plots in non-defaunated areas (WLP present). At the Ilha do Cardoso State Park (25°11′ S, 47°59′ W), we set up two plots: *IC–A* and *IC–B*. This protected island has 15,100 ha and is mostly covered with a lowland vegetation type. The density of WLP in this area is estimated in 13.55 ± 6.25 ind/km^2, accounting for ~80% of the biomass of mammals (Galetti et al., 2017). At Itamambuca (23°19′ S, 45°05′ W), we set up three plots: *ITA–A*, *ITA–B*, and *ITA–C*. This area harbors a submontane vegetation. It belongs to the protected area of Santa Virginia (17,000 ha) which pertains to the Serra do Mar State Park, the largest fragment of Atlantic rainforest (315,000 ha). The density of WLP in Santa Virginia is estimated in 3.35 ± 3.09 ind/km^2 and ~85% of the biomass of mammals (Galetti et al., 2017).

We set up six plots in defaunated areas (WLP absent). We established one plot in each of two forest fragments of semi-deciduous forest: Mata Santa Genebra, *SG* (22°49′ S, 47°07′ W; 252 ha) and at São José Farm, *SJ* (22°22′ S, 47°28′ W; ~230 ha). We also established four plots in continuous submontane forests: one at Intervales, *INT* (24°19′ S, 48°25′ W; 49,888 ha), and three at Vargem Grande (23°26′ S, 45°14′ W): *VG–A*, *VG–B*, and *VG–C*. Intervales belongs to a larger fragment at the Paranapiacaba mountains (~140,000 ha). Vargem Grande belongs to the Santa Virginia protected area. Although Vargem Grande and Itamambuca belong to

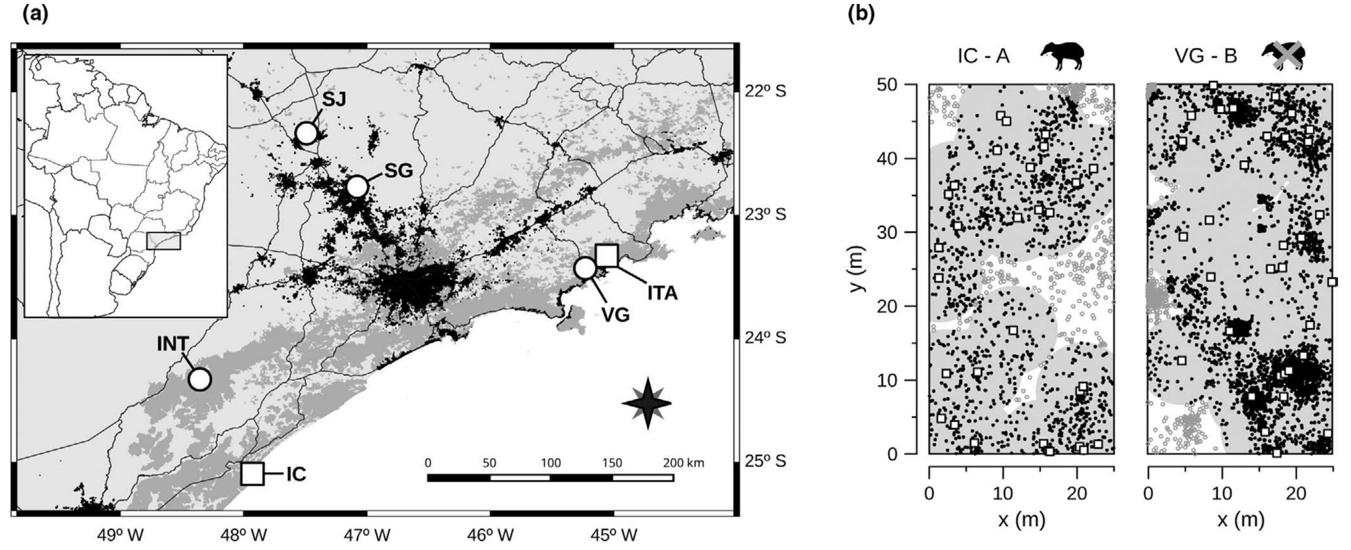

FIGURE 1 Study locations and plot setup. (a) Study locations. Non-defaunated areas (empty squares): Ilha do Cardoso (IC), Itamambuca (ITA). Defaunated areas (empty circles): São José (SJ), Santa Genebra (SG), Intervales (Int), and Vargem Grande (VG). Forest fragments are in dark gray, most important urban areas in black. (b) Examples of plots: on the left a plot with WLP at Ilha do Cardoso (IC-A), on the right a plot without WLP at Vargem Grande (VG-B). Square symbols denote adult trees. Filled and empty circles indicate seedlings within and outside a seed shadow of 6-m depicted by the gray areas

the same forest fragment, differences in hunting pressures and a busy highway separating them have led to the contrasting levels of defaunation. At the time of this study, the minimum time elapsed since WLP was declared extinct at each fragment is as follows: Santa Genebra, 13 years (Monteiro-Filho, 1995); São Jose, 11 years (Briani et al., 2001); Intervales, more than 18 years (Brocardo et al., 2012); and Vargem Grande, more than 7 years (Cruz, 2017; Galetti, unpublished data). See Tables S1 and S2 for a summary.

2.2 | Study design

All plots were located on flat terrain avoiding steep slopes and, in areas with similar soil moisture, avoiding waterlogged areas or more exposed areas due to less canopy coverage. To avoid edge effects on smaller forest fragments, the plots were placed near the center of the fragment (222 m and 170 m from the edge in SJ and SG, respectively). In addition, the chosen sites had no evidence of palm harvesting, so that the spatial distribution of the plants reflected the natural recruitment processes.

Plots consisted of a 25 × 50 m rectangular area (Figure 1b). We divided each plot into 1 m^2 cells, yielding a grid of 1,250 cells. Within each 1 m^2 cell, we counted the number of seedlings, saplings, and reproductive adults of *E. edulis*. For representative purposes, the location of each individual within the 1 m^2 cell was randomized, assigning an error to each spatial coordinate of $<\pm 1$ m, which is not relevant to the analyses performed.

Ontogenetic stages were identified based on the plant height, presence of evident apical stem, and evidence of reproductive events. Seedlings (~1 year old) were identified as those plants below 0.5 m (Wendling, 1998) and bearing a maximum of three leaves (de Carvalho, 1999). Saplings were identified as those individuals over this height, with a well-defined apical stem and without evidence of being reproductive (de Portela et al., 2011; Portela et al., 2010). Finally, those individuals showing any evidence of being reproductive (e.g., presence of inflorescence) were characterized as adults. Reproductive maturity in *E. edulis* usually begins when plants are 6–8 years old (Bovi et al., 1988; de Portela et al., 2011).

2.3 | Age structure

We tested the effects of WLP on the population age structure of *E. edulis* by using generalized linear models on each ontogenetic stage and using both its total and relative number of individuals as response variable. For the total number of individuals, we used a negative binomial distribution, and for the relative number, we used a quasibinomial distribution to account for overdispersion in the data.

2.4 | Plant spatial structure

We summarized the spatial patterns of each ontogenetic stage by exploring the spatial density distribution of plants from the same ontogenetic stage using the Pair Correlation Function (*g(r)*; Stoyan & Stoyan, 2014). This function explores the distance at which clustering or regularity operates by describing the expected density of points at distance *r* from any point. For a distance *r*, *g(r)* equals 1 if the frequency of points at that distance is the same as that expected under a random spatial distribution. If *g(r)* is above 1, the frequency of points at that distance is higher than the random model, and if *g(r)* is below 1, this frequency is lower than expected (see Note S1).

This function was constructed for distance bins of 1 m, overcoming the error associated with the spatial location of each point. We then compared this with a theoretical random point pattern by the construction of 95% CI envelopes obtained after 99 simulated point patterns. To correct for edge effects, we used the formula proposed by Wiegand and Moloney (2004).

2.5 | Spatial relationship between plant ontogenetic stages

We explored whether the presence/absence of WLP was associated with differences in the spatial relationship between the two early ontogenetic stages and adults. We constructed linear mixed-effects models using as response variable the cube-transformed distances between seedlings and the nearest adult and between saplings and the nearest adult separately (R/ *nlme* package; Pinheiro et al., 2017). Because these distances may be influenced by the overlap of seed shadows of nearby adults, we included as an independent variable the density of adults within a radius of 6 m around each seedling and sapling. This value corresponds to the 95th percentile of the distribution of distances from seedlings to the nearest adult in those plots without WLP. To account for differences in plant densities and spatial structure, we included plot identity as random effects variable. The best models were chosen based on the Akaike information criterion and analyses of variance.

We assessed how distance classes (from both seedlings and sapling to the nearest adult) differed between treatments. For each plot and ontogenetic pair comparison, we calculated the proportion of distances falling within distance bins of 1 m. Next, for each interval we compared the proportions obtained in the plots where WLP was present with those obtained in the plots without WLP. Due to the small sample size, comparisons were performed using a two-sample permutation test using asymptotic approximation (R/*perm* package; Fay & Shaw, 2010).

2.6 | Spatial patterns of recruitment

We analyzed the repulsion/attraction of seedlings and saplings to adults by constructing the bivariate version of the Pair Correlation Function ($g_{12}(r)$; Note S1). The observed values were compared with a null model describing a random recruitment pattern. To do so, we obtained 95% CI envelopes after 99 randomization of the spatial location of seedlings or saplings while keeping the original spatial location of adults.

We explored whether the spatial patterns of saplings followed the recruitment patterns of seedlings and whether these differed between plots with and without peccaries. To do so, we compared the observed $g_{12}(r)$ function between saplings and adults with a null model where the spatial distribution of saplings was randomized following the density of occurrence of seedlings in the plot.

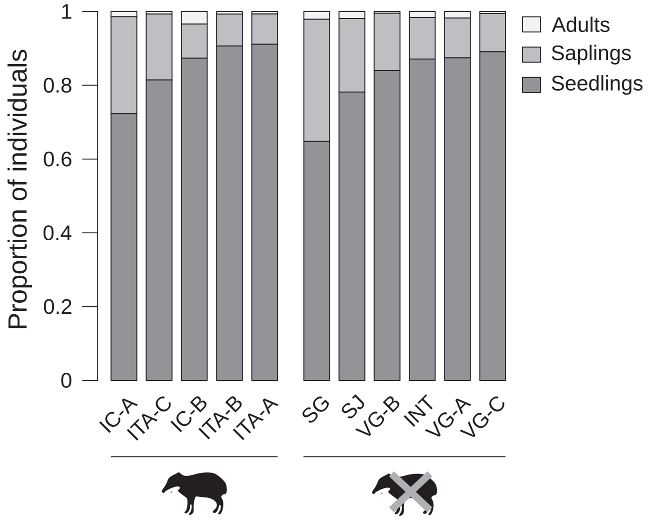

FIGURE 2 Age structure of *Euterpe edulis* in the studied plots. For each plot, stacked bars show the proportions of adults, saplings and seedlings. Full names of abbreviations are given in Figure 1

All spatial point pattern analyses were performed using the software PROGRAMITA (Wiegand & Moloney, 2004, 2014). Statistical models and plots were developed in R v. 3.4.3 (R Core Team, 2017).

3 | RESULTS

3.1 | Age structure

The number and proportion of individuals of each ontogenetic stage varied among plots (mean ± *SD*: 41.54 ± 17.98, adults; 552.27 ± 325.03, saplings; 3,136.36 ± 1,709.32, seedlings; Figure 2). We did not find evidence that the presence of WLP affected the total number of each ontogenetic stage (residual deviance $D = 11.25$, $df = 9$, $p = .13$ for adults; $D = 11.54$, $df = 9$, $p = .30$ for saplings; $D = 11.42$, $df = 9$, $p = .24$ for seedlings) neither in their relative number ($D = 0.05$, $df = 9$, $p = 1$ for adults; $D = 0.45$, $df = 9$, $p = .40$ for saplings; $D = 0.44$, $df = 9$, $p = .90$ for seedlings; Figure 2).

3.2 | Plant spatial structure

Adult trees from most of the plots followed a random spatial pattern. Only one plot with WLP present (IC-A) and one plot with WLP absent (SJ) showed a clustered distribution at short distances (<1 m in IC-A, and 3–5 and 7–9 m in SJ; Figure S1 and S2). In contrast, saplings and seedlings from all plots showed clustered spatial patterns. Saplings in plots with WLP present showed a spatial clustering below 3–9 m (6 ± 2.12) while in plots where WLP was absent this distance increased to 6–12 m (8.83 ± 2.48; Figures S1 and S2). For seedlings, this clustering augmented to 6–18 m (10.2 ± 5.76) in plots with WLP and to 10–20 m (14.67 ± 3.72) in plots without WLP (Figures S1 and S2).

TABLE 1 Results of linear mixed-effects models built on the cube-transformed distances from seedlings and saplings to the nearest adult tree

Ontogenetic pair	Parameter	estimate ± 1*SD*	*t*-value	*p*-value
Seedlings-nearest adult	Intercept	1.57 ± 0.03	63.25	<.001
	WLP	0.11 ± 0.04	2.97	.016
	Adult density	−0.06 ± 0.01	−78.84	<.001
	WLP × adult density	−0.03 ± 0.01	−17.67	<.001
Saplings-nearest adult	Intercept	1.61 ± 0.02	65.70	<.001
	WLP	0.17 ± 0.04	4.66	.001
	Adult density	−0.06 ± 0.01	−34.33	<.001
	WLP × adult density	−0.04 ± 0.01	−12.15	<.001

Note: WLP, presence/absence of white-lipped peccary; adult density, density of adults within a radius of 6 m around each seedling and sapling.

3.3 | Spatial relationship between plant ontogenetic stages

The best models in explaining the variation in spatial distance from both seedlings and saplings to the nearest adult were those that considered the presence of WLP, adult density within 6 m radius, and their interaction (Table S3). These models explained 33.26% and 36.20% of the variance (seedlings- and saplings-nearest adult, respectively) and revealed that the presence of WLP had a positive significant effect on the seedlings- and saplings-nearest adult pairwise distances (0.11 ± 0.04 and 0.17 ± 0.04, respectively; Table 1). In fact, average distances to the nearest adult were significantly higher in plots with WLP present than in plots without WLP, for both seedlings (1.5-fold higher, two-sample permutation test: |Z| = 2.14, *p* = .03) and saplings (1.3-fold higher, |Z| = 2.03, *p* = .04).

Areas with and without WLP differed in the distribution of distances between seedlings and the nearest adult. Specifically, below 2 m from any adult plant, plots without WLP showed higher proportions of seedlings than plots where WLP were present (|*Z*| = 2.21, *p* = .03 for bin 1 and |*Z*| = 2.20, *p* = .03 for bin 2; Figure 3a; but see Figure S3 for a comparison using true numbers). Regarding the spatial distance between saplings and the nearest adult, we found differences for the first meter (|*Z*| = 2.09, *p* = .036; Figure 3b), with more saplings in plots without WLP.

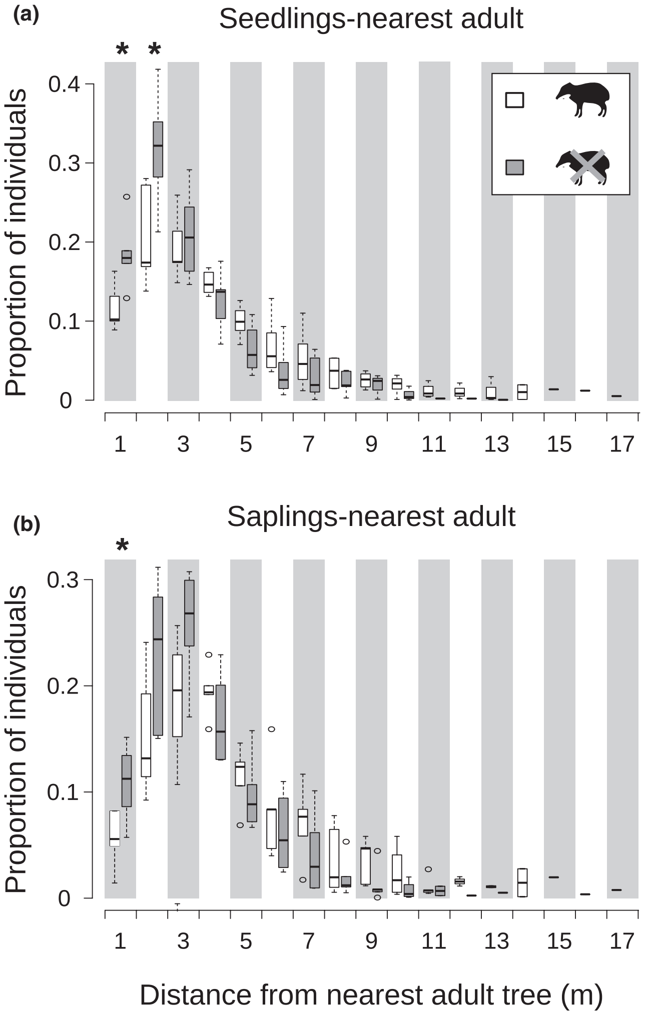

FIGURE 3 Distributions of distances to the nearest adult tree. (a) Seedlings-nearest adult tree. (b) Saplings-nearest adult tree. The proportion of individuals falling within each distance class are shown for plots with and without peccaries. Asterisks indicate significant differences

3.4 | Spatial patterns of recruitment

The bivariate Pair Correlation Function revealed that seedlings followed a clustered pattern within the first two meters from adult trees in most of the plots where WLP was present (4 out of 5; Figure 4a), whereas in plots without WLP this radius augmented to 8 m (i.e. 4–6 out of 6 plots showed a clustered pattern within this distance range; Figure 4c). In some of the plots without WLP, this pattern extended even to larger distances. Regarding the saplings, most plots with WLP present showed a random spatial pattern in relation to adult trees (Figure 4b). This pattern was not as evident in those plots without WLP; in some of these plots, a clustered pattern of saplings in relation to adult trees arose at the intermediate radius (3–13 m; Figure 4d).

Finally, the bivariate Pair Correlation Function between saplings and adult trees deviated from the null model defined by the spatial density of seedlings (Figure 5). These deviations did not show any clear contrasting pattern between treatments. However, values of g_{12} close to 1 indicate a tendency for seedlings to have a more random spatial distribution relative to adult trees (Stoyan & Penttinen, 2000). Consequently, differences between observed and null expectations were higher at those distances where seedlings occurred at highest densities, which mainly occurred in plots without WLP (e.g., VG-A: 5–10 m bins, Figure 5i; VG-B: 1–3 m bins, Figure 5j, or VG-C: most of the range, Figure 5k).

4 | DISCUSSION

The presence of white-lipped peccaries changed the spatial patterns of recruitment of *E. edulis*. However, such differences had no effect on the population age structure nor on the spatial distribution of adult palms. We found that the variance in age structure attributed to the presence of WLP was lower than that attributed to within group (ontogenetic stage) variability, indicating the absence of effect of WLP on the demography of *E. edulis*. This finding contrasts with other studies that demonstrated the important role of these animals in controlling the demography of other plant species by drastically diminishing the number of seedlings (Silman et al., 2003).

Factors involved in plant recruitment are multiple and frequently site-dependent: for example, predation by insects (Crawley, 1992), microenvironmental suitability (Gomez et al., 2004; Willson, 1988), intra- and interspecific competition (Dyer et al., 2008; Fowler, 1995), or multiple interconnected causes. In our study system, apart from WLP, other animals such as tapirs (*Tapirus terrestris*), agoutis (*Dasyprocta* spp.), small rodents and other ungulates prey upon seeds of *E. edulis*. In fact, in areas were WLP are locally extinct, small rodents can take over as the primary post-dispersal predators of *E. edulis* seeds, even overcompensating for the risk of predation by WLP (Fadini et al., 2009; Galetti et al., 2015). It is likely that this is happening in our study areas, due to the presence of some of these small rodents, and further evidences of their importance as predators of *E. edulis* seeds (Galetti et al., 2015).

The results of our models showed an overall effect of WLP on the spatial recruitment patterns of *E. edulis*. At first, this can be evidenced by an increase in the range of the spatial clustering of seedlings and saplings in those plots without WLP. This points to the role of WLP in shrinking the effective seed shadow of *E. edulis*. Furthermore, as previous studies have demonstrated, these animals concentrate their foraging activities under *E. edulis* adults where seed rain and seedling density are high (Keuroghlian & Eaton, 2009; Kiltie, 1981), we thus hypothesized that their removal would release early ontogenetic stages from part of the negative density-dependent effects. Our fine-grain analyses on the effects of WLP showed that the proportional distribution of seedlings and saplings at different distances from the nearest adult tree flattened under the presence of WLP, even showing significantly lower proportions of seedlings and saplings at very short distances from the nearest adult (<2 m and 1 m, respectively).

Our findings are similar to many others that demonstrate a correlation between proximity to source and density-dependent seed mortality (Comita et al., 2014; Hammond & Brown, 1998). However, they also contradict the suggestion that removal of seeds under adult trees by WLP could facilitate germination and establishment over short distances (Keuroghlian & Eaton, 2009). Seedling competition decreases the probability of survival and growth (Matos & Watkinson, 1998), and

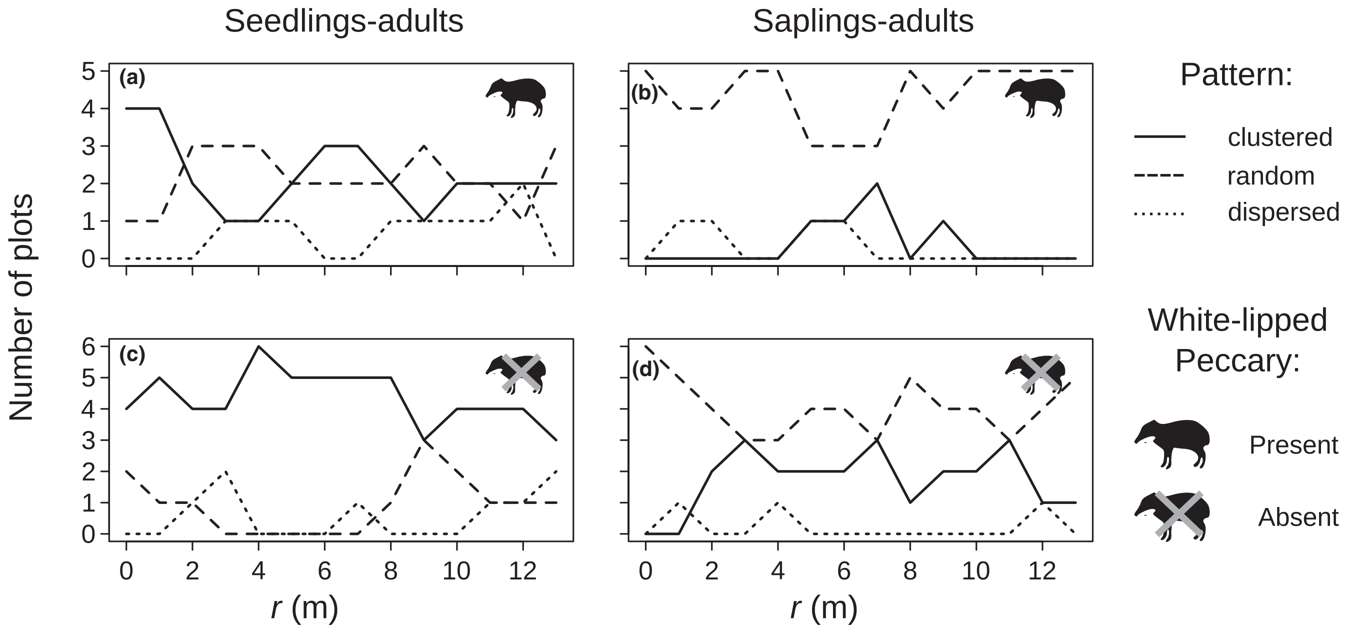

FIGURE 4 Patterns of attraction/repulsion. Panels show the number of plots that had clustered, random or dispersed spatial point patterns at a series of distance classes (*r*) from adult trees after the bivariate Pair Correlation Function

seed predation by herbivores may prevent negative density-dependent effects associated with bacteria and invertebrates (Bagchi et al., 2014) mainly because seedling competition decreases the probability of survival and growth (Matos & Watkinson, 1998). This latter hypothesis could be true, especially since seed predation by these herbivores may prevent density-dependent negative effects associated with bacteria and invertebrates (Bagchi et al., 2014). Nevertheless, in our peccary-free plots, small mammals that take on the role of major seed consumers may have contrasting predation patterns. In fact, some of the species found in these areas such as agoutis (*Dasyprocta* spp.) and

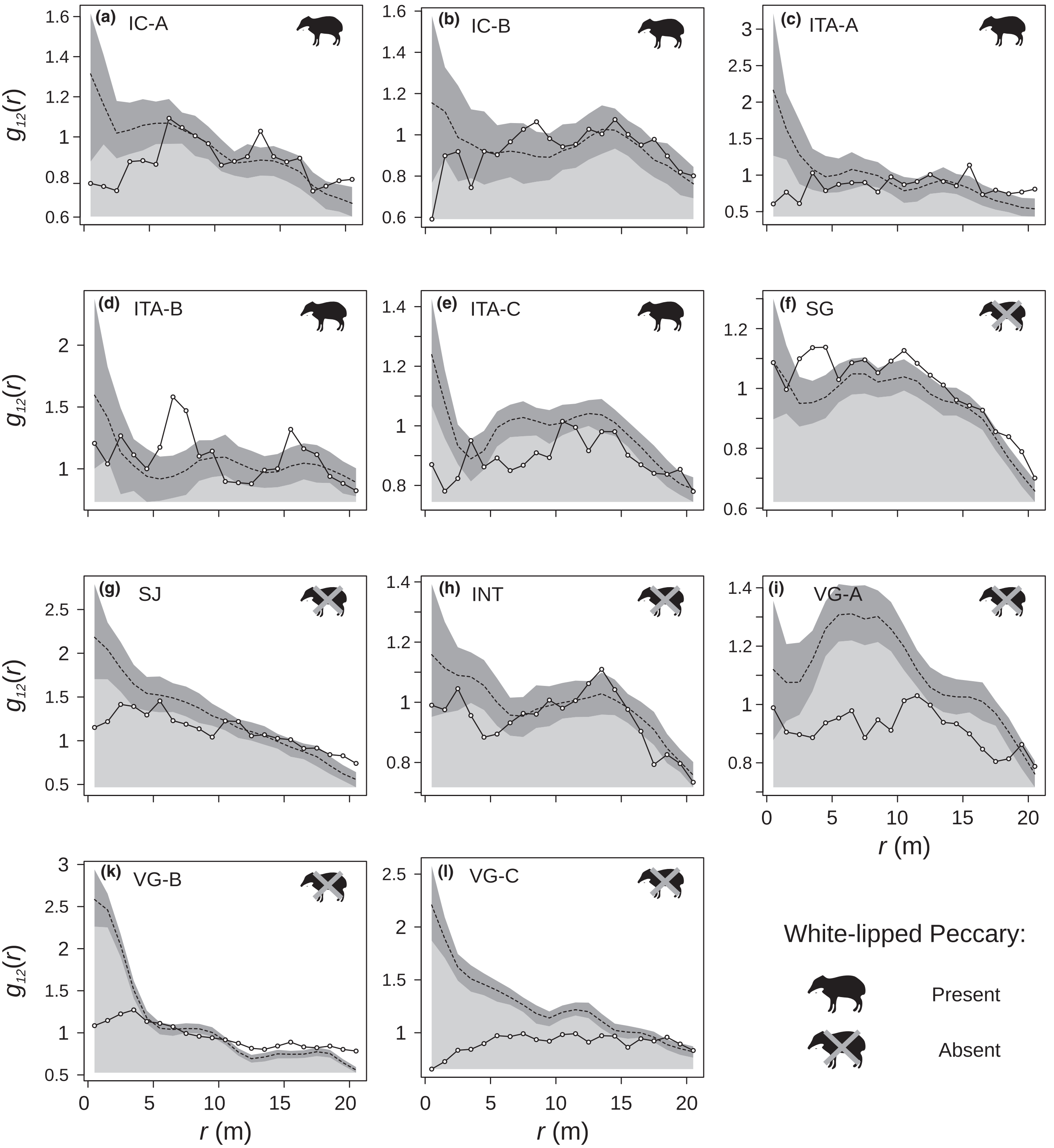

FIGURE 5 Spatial patterns of recruitment. Panels show the results from the bivariate Pair Correlation Function (g_{12}) between saplings and adult trees (solid lines and empty circles) at a series of distance classes (r). Envelopes correspond to the expected distribution of this function if the spatial distribution of saplings was completely determined by that of seedlings. Values below (light gray area) and above (white area) those envelopes, respectively, indicate a spatial relationship between saplings and adult trees that is relatively more random or more aggregated than expected. Full names of abbreviations are given in Figure 1

squirrels (*Sciurus* spp.) are known to scatterhoard seeds (Forget, 1990; Mendes et al., 2019; Paschoal & Galetti, 1995), which may explain the smoothing of the recruitment distances.

Overall, the presence/absence of WLP affected the patterns of spatial relationship between pairs of ontogenetic stages. In areas without WLP, the distance up to which seedlings tended to cluster significantly around adults was greater than in those areas where these were present. But more interestingly, it seems that the effects of WLP influence the spatial recruitment patterns of further ontogenetic stages. In areas with WLP, saplings showed a generalized pattern of random spatial distribution within a 13 m radius away from adults, whereas in areas without WLP this spatial relationship varied between random and grouped, depending on the plot. These contrasting results suggest that the effect of these large herbivores compensates dispersal and survivorship of seedlings (McCanny, 1985), resulting in scattering of saplings in the landscape. On the other hand, in defaunated areas this compensation occurred to a lesser extent, as saplings were more prone to be found clustered around adults. Interestingly, those defaunated plots showing a greater randomization of the distribution of saplings were located in larger forest fragments (Intervales and Vargem Grande). These areas correspond to those where defaunation of large mammals is less severe (Galetti et al., 2009; Table S2), and therefore, it may be possible that other species such as tapirs (*Tapirus terrestris*) may be foraging on *E. edulis* seeds in a manner similar to WLP.

The tendency to randomization of the spatial pattern of late ontogenetic stages probably required more drastic changes in the defaunated areas. For example, in some of the plots without WLP (e.g., VG-A, VG-B, and VG-C, Figure 5i, j and k), the change from seedling density to that of saplings was especially high at those distances to the nearest adult where the density of seedlings was highest. The paradox of low recruitment under adult plants, where seed density is higher, could be explained by the density-dependent action of other negative factors affecting recruitment, as stated in the Janzen–Connell theory. For instance, although less important than herbivory, pathogens are one of the factors that negatively affect recruitment in *E. edulis* (Rother et al., 2013). It could happen that under very high densities of seedlings, this attack is enhanced, as has been demonstrated in many other tropical tree species (Augspurger, 1984; Goodale et al., 2014). High densities also increase intraspecific competition that hinders seedling establishment by affecting the development of aerial parts in early stages, as has been previously reported for *E. edulis* (Pizo & Simão, 2001). Whatever the mechanism behind this, the negative effects associated with high densities of conspecifics are generally strongest in the transition from seedling to sapling (Comita et al., 2014; Terborgh et al., 2008).

Our results indicate that although seed predation and trampling by WLP do not seem to significantly affect the age structure of the population nor the spatial distribution of adult *E. edulis* stems, they can regulate the fine-scale spatial recruitment patterns of this palm species. In areas where WLP has become extinct, the fauna that take over the role as the main seed predator of this palm—mostly small mammals—do not seem to have the same effect on the recruitment pattern. We think that these results offer the opportunity to further research into the ecological and evolutionary effects of defaunation. For example, in areas heavily impacted by defaunation, the decrease in average seed size of *E. edulis* associated with the local extinction of large seed dispersers could have repercussions on the post-dispersal phase, mainly in areas where small seed predators have taken over the role of main seed predators. Overall, this highlights the influence of large-bodied threatened herbivores on the spatial patterns of plant regeneration, since defaunation is one of the major drivers of plant demography (Galetti & Dirzo, 2013) and plant regeneration is a critical factor in maintaining species diversity in tropical forests (Villar et al., 2020).

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DATA AVAILABILITY STATEMENT

Data openly available from the Figshare digital repository https://doi.org/10.6084/m9.figshare.12401612

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SUPPORTING INFORMATION

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