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Animal–Plant Interactions Under Defaunation: Consequences for Amazonian Trees of Commercial Interest

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ABSTRACT

The decline of medium- and large-bodied terrestrial mammal populations can compromise key ecological processes such as seed dispersal. We conducted an exclusion experiment to simulate a defaunation gradient, monitoring the removal of 1800 seeds from six plant species of commercial interest in the Amazon Forest. Overall, mammal exclusion significantly reduced seed removal, particularly under severe exclusion conditions. However, this effect was species-specific. Only *Lecythis lurida*, the species with the largest seeds, showed a significant reduction in removal under severe defaunation. *Proechimys* spp. interacted with most seeds in all experimental treatments, except for *L. lurida*, whose seeds were removed only by *Dasyprocta croconota*. While *Proechimys* spp. likely acts as a seed predator for all tested species, *D. croconota* can contribute to seed dispersal and consequently to the recruitment of a variety of plant species. Our findings reinforce that while defaunation impacts seed removal, its effects depend on plant traits and the identity of dispersers. The loss of terrestrial mammals may compromise long-term plant recruitment, especially for species that rely on larger mammals for effective seed removal. The loss of ecological interactions may jeopardize the sustainable supply of timber and non-timber products, directly affecting the income and food security of local traditional cooperatives in the Amazon.

RESUMO

O declínio das populações de mamíferos terrestres de médio e grande porte pode comprometer processos ecológicos essenciais, como a dispersão de sementes. Realizamos um experimento de exclusão simulando um gradiente de defaunação, monitorando a remoção de 1.800 sementes de seis espécies de plantas de interesse comercial na Floresta Amazônica. De modo geral, a exclusão de mamíferos reduziu significativamente a remoção de sementes, particularmente em condições de exclusão severa. No entanto, esse efeito foi específico para cada espécie. Apenas *Lecythis lurida*, a espécie com as maiores sementes, apresentou redução significativa na remoção sob defaunação severa. *Proechimys* spp. interagiram com a maioria das sementes em todos os tratamentos experimentais, exceto para *L. lurida*, cujas sementes foram removidas apenas por *Dasyprocta croconota*. Embora *Proechimys* spp. provavelmente atue como predador de sementes para todas as espécies testadas, *D. croconota* pode contribuir para a dispersão de sementes e, consequentemente, para o recrutamento de diversas espécies de plantas. Nossos resultados reforçam a ideia de que, embora a defaunação impacte a remoção de sementes, seus efeitos dependem das características das plantas e da identidade dos dispersores. A perda de mamíferos terrestres pode comprometer o recrutamento de plantas a longo prazo, especialmente para espécies que dependem de mamíferos maiores para a remoção eficaz de sementes. A perda de interações ecológicas pode colocar em risco o fornecimento sustentável de produtos madeireiros e não madeireiros, afetando diretamente a renda e a segurança alimentar de cooperativas tradicionais locais na Amazônia.

1 | Introduction

Tropical forests harbor more than twice as many known species as any other terrestrial biome on Earth (Pillay et al. 2022). However, in recent decades, they have experienced severe biodiversity losses, primarily due to population declines and local extinctions of vertebrates, a process known as defaunation (Dirzo et al. 2014; Galetti et al. 2017; Gardner et al. 2019). Defaunation can disrupt ecological interactions and compromise key functions that regulate critical ecosystem functions, such as seed dispersal and predation (Galetti, Bovendorp, and Guevara 2015; Fedriani et al. 2020), ultimately affecting plant mortality and recruitment (Villar and Medici 2021). Despite its vastness and biodiversity, the Amazon has not been exempt from this process, with reports of defaunation driven by expanding anthropogenic activities (Peres and Palacios 2007; Rosa et al. 2021).

In tropical forests, approximately 90% of plant species depend primarily or exclusively on frugivorous animals for seed removal (Jordano 2000). Seed removal by animals typically leads to two possible outcomes: dispersal—when the seed is transported and deposited away from the parent plant (with or without prior ingestion)—or predation—when the seed's embryo is damaged during consumption (Howe and Smallwood 1982). While frugivores may act as seed predators when consuming fruits, they often provide the service of seed dispersal by moving viable seeds over long distances, which can enhance germination and recruitment success (Jordano and Godoy 2002; Beck et al. 2013; Squinzani et al. 2022). Medium- and large-bodied mammals play a crucial role in this process, as many species ingest whole fruits and seeds and defecate the seeds intact, often far from the parent plant (Beckman and Sullivan 2023). This ability to handle and transport large seeds is closely linked to body size, as smaller animals typically cannot consume large seeds without damaging them through mastication (Chen et al. 2017). However, small mammals can also carry seeds without ingestion, eventually dropping or caching the seeds, thus dispersing them through stomatochory (McConkey et al. 2024). Additionally, larger seeds are expected to be more attractive to frugivores and seed predators due to the higher nutrient content of the fruits or seeds themselves (Dirzo and Mendoza 2007; Dylewski et al. 2020). Therefore, the absence of medium- and large-bodied mammals may compromise the dispersal and recruitment of large-seeded plant species in defaunated areas (De Paula et al. 2018). In Afrotropical forests, for instance, Rosin and Poulsen (2016) observed that the removal of terrestrial mammals significantly reduced seed removal and increased predation rates, leading to lower seedling establishment. Studies in Neotropical forests have shown that the absence of large mammals may favor an increase in the abundance of small rodents (Wright 2003; Galetti, Neves, et al. 2015; Bovendorp et al. 2018). These animals tend to act more as seed predators than as dispersers (De Mattia et al. 2004), which can intensify predation pressure and negatively impact plant recruitment, especially for species whose seeds are primarily dispersed by large terrestrial mammals.

Reductions in seed dispersal in defaunated areas can, in the medium term, affect several vital ecological processes for plant life, such as establishment, recruitment, and consequently, impact the populations of many plant species (Villar and Medici 2021; Beck et al. 2013), including those of high commercial value such as timber species (Rosin and Poulsen 2016). Changes in plant recruitment may lead to the replacement of species whose seeds are removed by medium- and large-bodied frugivores, often of greater commercial value, by species of lower commercial interest, whose seeds are dispersed by wind, small mammals, or birds (Peres et al. 2016). This shift may have negative economic consequences for local and traditional communities that depend on both timber and non-timber forest products.

The effects of defaunation have been widely studied in highly fragmented biomes such as the Atlantic Forest (Souza et al. 2022; Villar and Medici 2021), where successive local extinctions have already altered ecological interactions. These studies have found consistent evidence of the direct and indirect impacts of fauna loss on seed removal and forest regeneration, such as reduced seed removal (Culot et al. 2017) and increased seed mortality (Galetti, Bovendorp, and Guevara 2015). However, most of this research has focused on a narrow set of plant groups, particularly palms and conifers (Culot et al. 2017; Galetti, Bovendorp, and Guevara 2015; Brocardo et al. 2018; Meiga and Christianini 2020; Squinzani et al. 2022).

Despite the Amazon's high biodiversity, experimental studies assessing how terrestrial mammal defaunation alters key ecological proceses remain scarce. To our knowledge, only two studies have addressed this issue using defaunation experiments. Beck et al. (2013), working in the Peruvian Amazon, found that defaunation increased seedling density and cover, indicating long-term shifts in forest dynamics and tree community structure. More recently, Batista et al. (2025) observed a substantial reduction in ungulate behaviors such as trampling, feeding, defecation, and bioturbation in defaunated areas. They also found that small mammals could not compensate for the loss of these functions, pointing to significant disruptions in ecosystem processes. However, no study to date has assessed how defaunation affects seed removal of plant species with commercial value in the Amazon. Understanding these interactions is essential for anticipating the ecological impacts of fauna loss, especially in a biome that remains relatively intact but is under increasing pressure. This knowledge is particularly relevant for assessing how reduced seed removal in defaunated areas may affect plant recruitment, with direct implications for fauna conservation and the sustainability of forest management practices—both timber and non-timber—involving commercial species in the region.

In this study, we employed a well-established exclusion plot model, experimentally simulating the exclusion of medium and large-sized terrestrial mammals. Plots followed an exclusion gradient, from control (no exclusion) to the most severe (total exclusion) (Galetti, Bovendorp, and Guevara 2015; Souza et al. 2022; Villar and Medici 2021; Batista et al. 2025), that experimentally evaluate the effects of terrestrial mammal defaunation on seed removal of commercially important Amazonian plant species. Generally, seeds are considered as removed when it is not possible to determine whether they have been dispersed or preyed upon by vertebrates during each survey. However, with the aid of camera traps, we were able to describe the behavior of animals interacting with seeds and infer whether they could have been dispersed or preyed upon.

Specifically, our objectives were: (1) to test how defaunation affects the removal of seeds from plant species of commercial interest, especially for species with larger seeds, and (2) to evaluate how the small-size rodent *Proechimys* spp. interact with seeds of plant species with different sizes—an understudied aspect of seed removal dynamics. We hypothesized that in environments where we experimentally simulated defaunation, the dispersal and successful germination of seeds of commercially valuable plant species would be negatively affected, resulting in reduced seedling recruitment because of the absence of medium and large-bodied mammals. We also expected that in the absence of seed removal, the probability of seeds being removed to suitable germination sites, whereas the remaining seeds would end up being attacked by other biotic agents, such as fungi and borer insects, especially for species with larger seeds.

2 | Methods

2.1 | Study Area

We conducted this study in the Tapajós National Forest (FNT), Pará, Brazil (Figure 1). The FNT is a sustainable-use protected area covering 527,319 ha, predominantly composed of dense terra firme rainforest, characterized by emergent trees reaching over 50 m in height, such as the *Bertholletia excelsa* and *Hymenolobium petraeum* (ICMBio 2019). The climate is classified as Am (tropical monsoon) under the Köppen system, with a mean annual temperature of 25°C and average precipitation of 2110 mm (INMET 2021).

Although mature forest predominates in the FNT, it is influenced by selective logging through a Reduced Impact

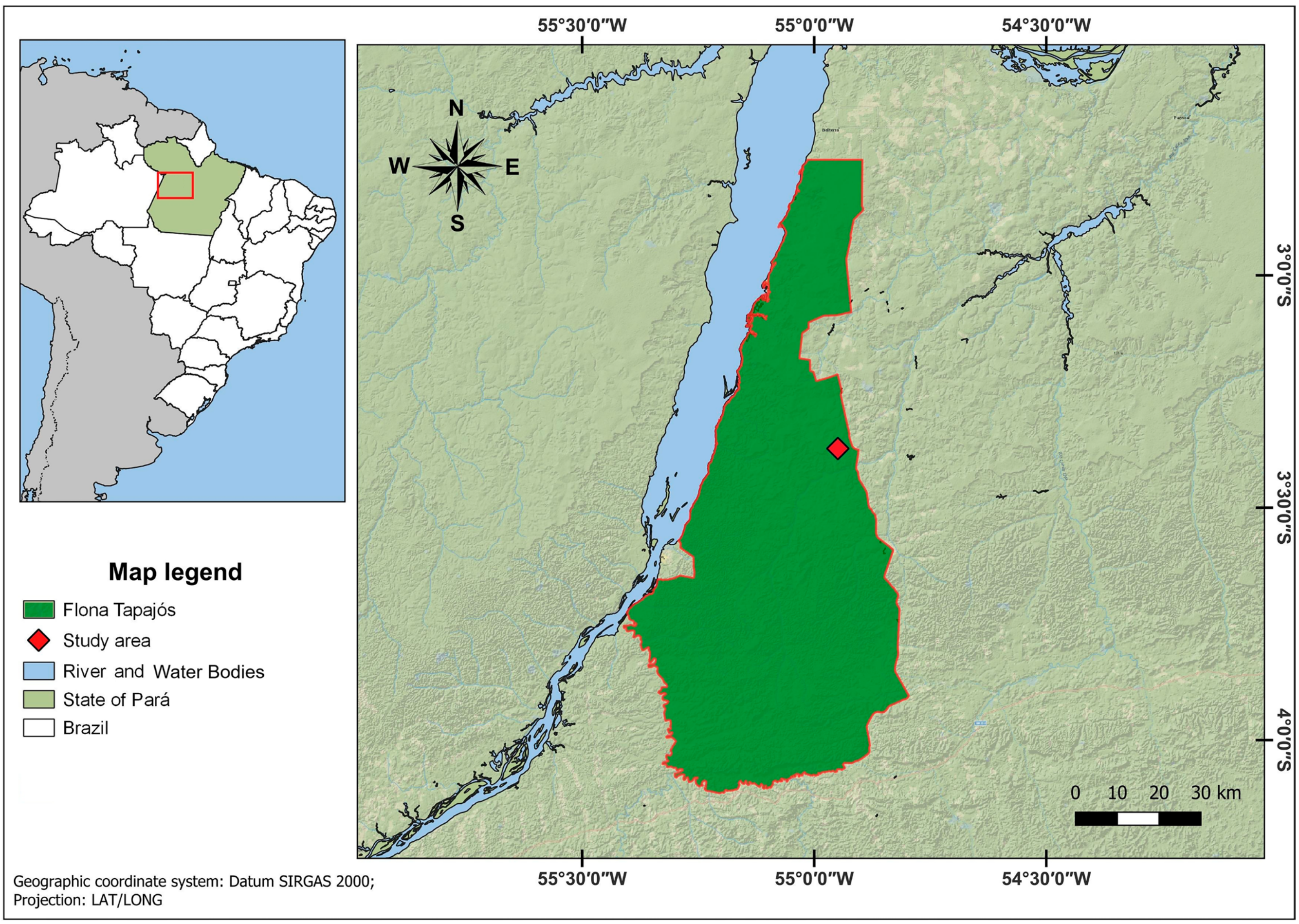

FIGURE 1 | Location of the study area within the Tapajós National Forest (FLONA Tapajós), Brazilian Amazon.

TABLE 1 | Seed traits of commercially important plant species used in the seed removal experiment across a gradient of terrestrial mammal defaunation in the Tapajós National Forest. Commercial use of the studied species: Nut consumption (NC), essential oils (EO), pulp and palm heart consumption (PPC), timber harvesting (TH).

Scientific name	Common name	Commercial use	Length (~cm)	Mass (~g)	Fruiting period (month)	Germination (day)
Bertholletia excelsa	Brazil nut	NC	4.1 (3.2–5.8)	5	January to May	~18 (month)
Carapa guianensis	Crabwood	EO	4.8 (3.8–6.2)	25	April to July	~30 (day)
Euterpe oleracea	Açaí palm	PPC	1.2 (0.7–1.5)	1.5	All year	~20 (day)
Hymenaea courbaril	Brazilian cherry	TH	3.5 (3–4)	3.5	June to September	~15 (day)
Lecythis lurida	Jarana	TH	8 (6–9)	30	March to May	~30 (day)
Manilkara huberi	Maçaranduba	TH	1.8 (1.2–2.4)	1.7	January to May	~6 (month)

Logging (RIL) forest management plan implemented by the Tapajós National Forest Mixed Cooperative (COOMFLONA). Commercially harvested species include *Hymenaea* spp., *Lecythis lurida*, and *Manilkara* spp. Additionally, non-timber products such as *Carapa guianensis* and *Bertholletia excelsa* are collected, along with essential oils, including *Copaifera* spp. (ICMBio 2019).

We established our experiment to simulate experimental defaunation in a non-managed forest area, located approximately 2 km from the nearest logging zone, near the COOMFLONA operational base (3°22′01.29″S, 54°57′04.73″W). Previous studies at the site have documented a diverse community of medium- and large-bodied granivorous and herbivorous mammals, including *Cuniculus paca*, *Dasyprocta croconota*, *Dicotyles tajacu*, *Mazama americana*, *Passalites nemorivagus*, and *Tapirus terrestris*, as well as top predators such as *Panthera onca* and *Puma concolor* (Rosa et al. 2021; Brocardo et al. 2023).

2.2 | Plant Species Selection

We assessed the effects of terrestrial mammal defaunation on seed removal from six commercially important plant species: *B. excelsa*, *C. guianensis*, *E. oleracea*, *H. courbaril*, *L. lurida*, and *M. huberi* (see Table 1; Data S2). Species selection was based on (1) commercial importance (timber and non-timber) in the Amazon (ICMBio 2019); (2) local availability of viable seeds (minimum of five adult trees, with at least 700 viable seeds per species); (3) known use as food resources by local fauna (Bodmer 1991; Galetti, Guevara, et al. 2015); and (4) variation in seed size and weight, ranging from 1.1 g (*M. huberi*) to 30 g (*L. lurida*), and from 1.2 cm (*E. oleracea*) to 9 cm (*L. lurida*) (Table 1).

Seed mass and size for *B. excelsa*, *C. guianensis*, and *L. lurida* were obtained from published sources (Carvalho 2014). For *E. oleracea*, *M. huberi*, and *H. courbaril*, we measured seeds in the laboratory. For each species, 100 depulped and cleaned seeds from at least five individuals were weighed using a precision scale and measured using a digital caliper.

2.3 | Exclusion Plots

We used experimental exclusion plots (5 × 10 m) to assess the effects of medium- and large-bodied mammal defaunation on seed removal. The experiment included 10 blocks spaced at least 500 m apart. Each block contained three plots representing defaunation treatments: (1) Control—plot marked with stakes at the corners and freely accessible to all terrestrial species; (2) Partial exclusion—plot fenced with steel mesh (5 × 10 cm), suspended 20 cm above the ground to allow access by medium-sized mammals (e.g., *C. paca*, *D. croconota*) while excluding large mammals (e.g., *T. terrestris*, *M. americana*); and (3) Severe exclusion—plot fenced with mesh buried 30 cm deep, excluding both medium- and large-bodied mammals (*T. terrestris*, *M. americana*, *T. pecari*, *D. tajacu*). Only arboreal and climbing mammals (e.g., primates, *Guerlinguetus* spp., *Didelphis* spp.), as well as small rodents (e.g., *Proechimys* spp.), had access to all treatments, including severe exclusion.

The three plots within each block were 10–30 m apart to ensure similar abiotic conditions (Figure 2). Each plot contained a 1 × 1 m subplot marked with PVC pipes where seed experiments were conducted.

2.4 | Seed Removal and Fate Experiment

We conducted the experiment during the rainy season (April–July 2022), coinciding with the fruiting period of selected species. We collected seeds in FNT, from at least five fruiting trees per species. For *H. courbaril* seeds, which have pulp adhered to them, we removed the pulp manually after water immersion and then sun-dried the seeds for approximately 6 h. *E. oleracea* seeds were collected from a plantation near the FNT and mechanically depulped without visible damage. The seeds of the remaining species (*B. excelsa*, *C. guianensis*, *L. lurida*, and *M. huberi*) were collected after being naturally shed and required no depulping, as they are dry seeds. We excluded all damaged or infested seeds.

Our experiment included a total of 1800 seeds from six plant species. Initially (April to July of 2022), the experiment started with 1500 seeds from five species, distributed in plots with 50

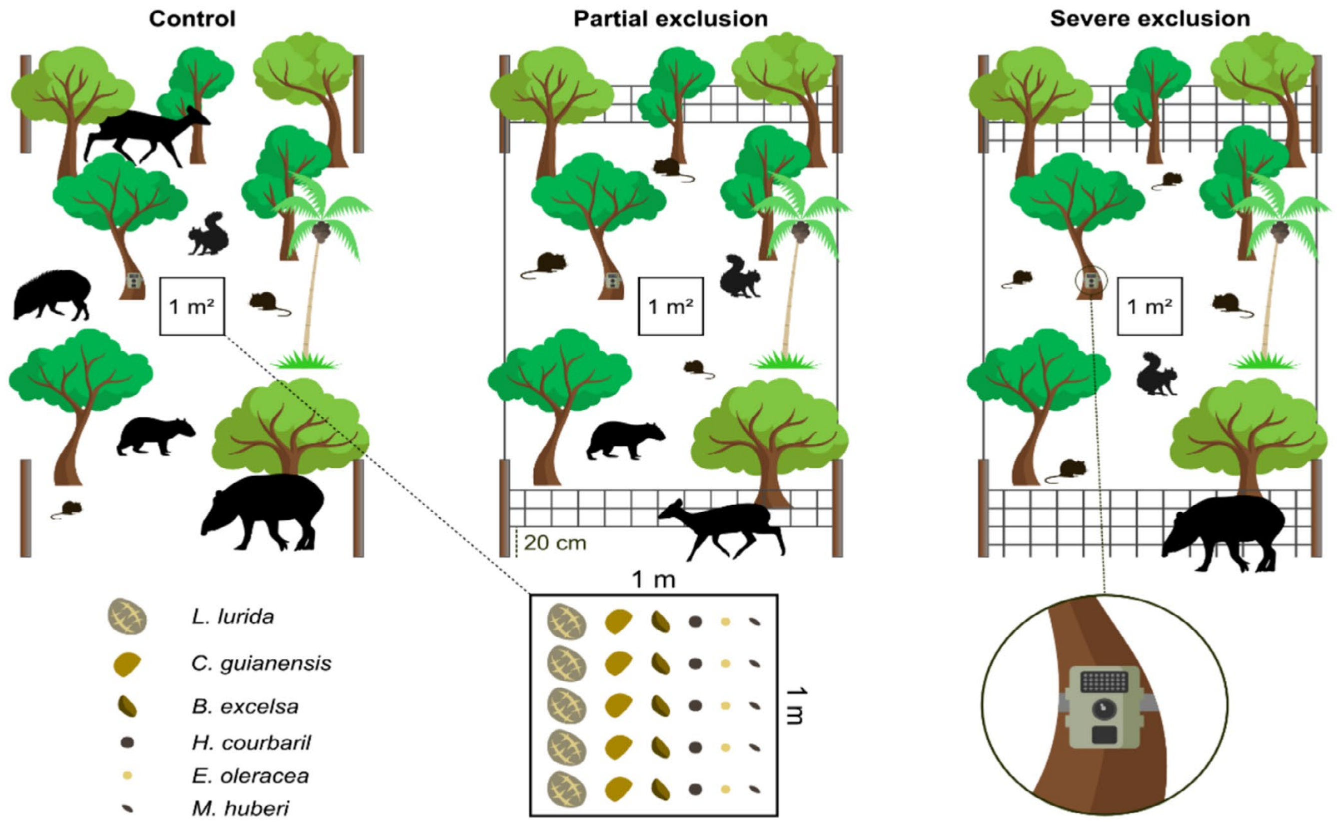

FIGURE 2 | Schematic representation of the exclusion experiment to experimentally simulate a defaunation gradient in the Tapajós National Forest.

seeds each (10 seeds per species per 1 m^2 subplot). The seeds were arranged in parallel rows on bare soil, spaced 10 cm apart within and between rows, with each row corresponding to a different species. Because fruits of *H. courbaril* were not available simultaneously with the other species, we added 300 seeds (10 seeds per plot, with two rows of five seeds each) of this species to the experiment in August. Although the availability of more seeds/species can attract more consumers or satiate frugivores, the similarity of the results among plant species in our experiments suggests that this is unlikely (see Section 3).

We inspected plots every 10 days for 70 days. For each seed, we recorded its fate: (1) removed; (2) predated by invertebrates (e.g., boring insects); (3) infected by fungi; or (4) germinated. Seeds were considered removed if missing or found with mammal tooth marks. For small seeds, shell fragments inside exclusion treatments helped confirm mammal removal. Germination was recorded when the radicle exceeded 2 cm or showed leaf sprouting. Frequently, seeds that were considered germinated were also later removed or still predated by fungi or insects. Thus, they were included in more than one category in the study. However, germination was not the primary focus of this study, as the experiment duration was insufficient to evaluate all species. For example, among the studied species, germination can take an average of up to 20 days for *E. oleracea* seeds (personal observation), to 6 months for *M. huberi* seeds (Cruz 2016) and 18 months for *B. excelsa* (Carvalho 2014). The experiment ended after two consecutive visits with no seed removal, and the remaining seeds were considered unviable due to fungal or invertebrate predation.

2.5 | Terrestrial Mammal-Seed Interactions

We installed one camera trap (Bushnell 12Mp NatureView Cam Essential HD Low Glow) per subplot, directed at the seed area (Figure 2). With only 15 cameras available, we randomly selected five blocks (15 plots) for each monitoring cycle. Every 10 days, corresponding with seed inspections, we rotated the cameras to ensure coverage across all blocks. Cameras alternated between sets of five blocks every 10 days, repeating the cycle throughout the 70-day study. In total, we accumulated 660 camera trap-days. Cameras were set to record 20-s videos with 10-s intervals. Species were identified using Rosa et al. (2021).

The animals' behavior was categorized into four classes, based on video data from camera traps: Non-interactive behavior (NB) – animals passing by without interacting with seeds; Interactive behavior (IB) – animals sniffing or handling seeds without removal; Dispersal behavior (DB) – seed removal from the plot (which could or could not result in seed dispersal); and Predation behavior (PB) – consumption of seeds within the plot. Notably, seeds that had IB were subsequently counted as removed after their removal.

2.6 | Data Analysis

To test whether defaunation influenced seed removal, we used generalized linear mixed models (GLMMs). First, we analyzed total seed removal (all species combined), followed by separate

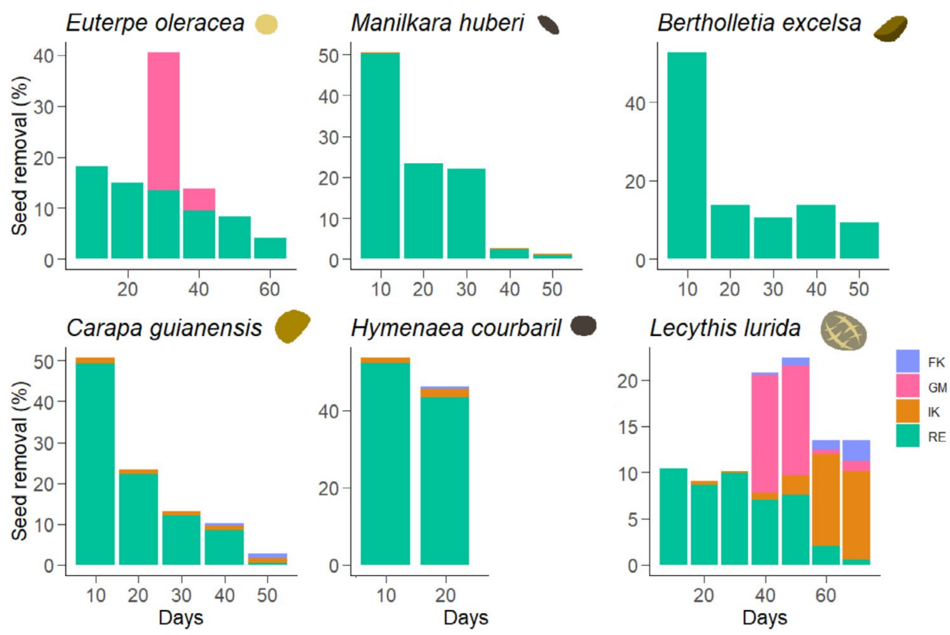

FIGURE 3 | Fate of seeds within the experiment simulating defaunation over 70 days by plant species. Seeds were categorized as: Removed (RE), Invertebrate-Killed (IK), Fungal-Killed (FK), or Germinated (GM).

analyses per species. The response variable was the number of seeds removed per plot, and the predictor was defaunation treatment (control, intermediate, severe). Block was included as a random effect, as each block contained all three treatments. Analyses were performed using the glmmTMB function from the glmmTMB package (Bolker 2023).

To evaluate interactions between mammals and seeds, we focused solely on *Proechimys* spp. due to the limited number of video records. These small-sized rodents weigh on average 250 g (Paglia et al. 2011). And are known to interact with various plant species in tropical forests via seed removal (Carreira et al. 2020). Specifically, for this analysis, the cameras allowed us to categorize the records into dispersed seeds and predated seeds and additionally classified seeds by size: (1) Small (≤2 cm): *E. oleracea*, *M. huberi*; (2) Medium (2.1–5 cm): *B. excelsa*, *C. guianensis*, *H. courbaril*; and (3) Large (>5.1 cm): *L. lurida*. We built three GLMMs, one per seed size class, with number of *Proechimys* spp. interactions as the response and defaunation treatment as the predictor. Block was included as a random effect. We used the glmer.nb function from the lme4 package with negative binomial distribution, which best fit the data. All analyses were conducted in R version 4.1.2 (R Development Core Team 2024), and plots were created using ggplot2 (Wickham 2016).

3 | Results

3.1 | Seed Removal and Fate

Of the 1800 seeds monitored over 70 days, 89.6% ($n = 1614$) were removed by terrestrial mammals. Overall, seed removal was highest in the control (571 seeds; 95.1%) and partial exclusion plots (563 seeds; 93.8%), and considerably lower in the severe exclusion plots (480 seeds; 80%). Seed removal by terrestrial mammals occurred mostly within the first 10 days of the experiment for most small- and medium-seeded species, with an average of 50% removed during this initial period. Exceptions were *E. oleracea*, with only 24.6% removal in the first 10 days, and *L. lurida*, with just 13% removed.

Among the seeds remaining after this period, most were later removed by mammals or attacked by fungi or invertebrates, with no evidence of germination. Exceptions were again *E. oleracea*, which had 36.6% of its seeds germinate between days 20 and 30, and *L. lurida*, with 16.3% germinating between days 30 and 40 (Figure 3). Our analysis revealed that defaunation had a significant effect on seed removal, with a marked reduction in the proportion of removed seeds in areas with lower terrestrial mammal presence ($\chi^2 = 63.403$; df = 2; $p < 0.001$; Figure 4).

In control plots, consumption by invertebrates (13 seeds; 2.1%), fungi (2 seeds; 0.3%), and germination (64 seeds; 10.6%) accounted for only a small fraction of the total. Partial exclusion showed a similar pattern: 4% ($n = 24$) of seeds were consumed by invertebrates, 0.6% ($n = 4$) by fungi, and 10.8% ($n = 65$) germinated. In contrast, in severe exclusion plots, the proportion of seeds with evidence of attack by invertebrates was 13% ($n = 78$), fungi (3.1%; $n = 19$), as well as those that germinated (16.5%; $n = 99$), was higher (Figure 5). Notably, however, 76.7% ($n = 76$) of germinated seeds in severe exclusion plots were later removed, indicating that initial germination does not guarantee protection from predation by either terrestrial mammals or invertebrates (see Data S1).

Except for *L. lurida*, seed removal for all plant species showed no significant variation across treatments: *E. oleracea* ($\chi^2 = 0.183$; df = 2; $p = 0.911$), *M. huberi* ($\chi^2 = 0.000$; df = 2; $p = 1.000$), *H. courbaril* ($\chi^2 = 0.001$; df = 2; $p = 0.968$), *B. excelsa* ($\chi^2 = 0.000$; df = 2; $p = 1.000$), and *C. guianensis* ($\chi^2 = 4.010$; df = 2; $p = 0.134$), *L. lurida* ($\chi^2 = 108.861$; df = 2; $p < 0.001$) (Figure 6). Overall, seed removal was high throughout the experiment, although this result was largely driven by the significantly lower removal of *L. lurida*, the species with the largest and heaviest seeds, in severe exclusion plots compared to control and partial exclusion plots. (Figure 6).

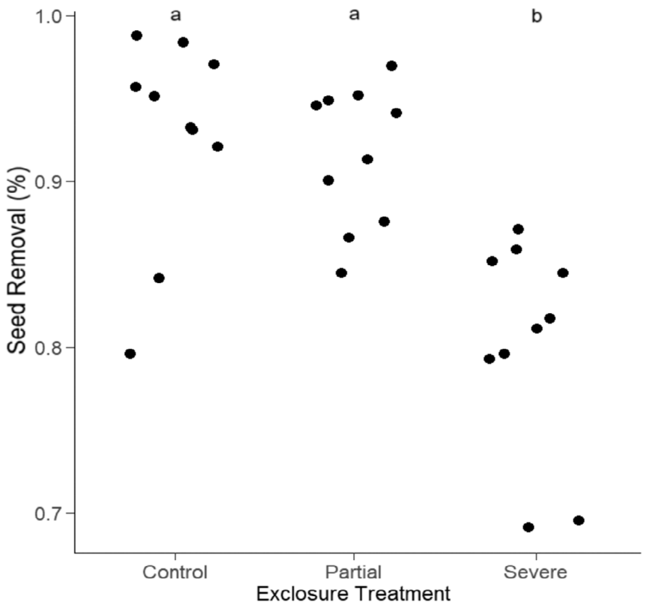

FIGURE 4 | Proportion of seeds removed by terrestrial mammals in each treatment of the defaunation gradient (Control, Partial Exclusion, Severe Exclusion). Each dot represents seed removal in one experimental plot (n = 10 per treatment). Identical letters indicate non-significant differences; different letters indicate significant differences.

3.2 | Terrestrial Mammal-Seed Interactions

We recorded 469 videos across all treatments during the experiment (Control, Partial exclusion, and Severe exclusion), identifying seven terrestrial mammal groups: small marsupials (Didelphidae), *C. paca*, *D. croconota*, *Dasypus* sp., *Didelphis* sp., *Guerlinguetus* spp., and *Proechimys* spp. Of these, only three taxa actively interacted with seeds: *D. croconota*, *Guerlinguetus* spp., and *Proechimys* spp., with a total of 205 interactions.

Of the total videos recorded, 43.9% (n = 206) consisted of non-interactive behaviors, in which animals only moved through the plots without engaging with the seeds. Interactive behavior (sniffing or handling, without dispersal) accounted for 12.4% (n = 58). Seed dispersal and predation behaviors accounted for 33% (n = 155) and 10.7% (n = 50), respectively (Figure 7).

Among the species observed interacting with seeds, *Proechimys* spp. showed both dispersal and local predation behaviors (n = 143) and interacted with all six plant species. We recorded 29 dispersal events and 26 predation events with small-seeded species (*E. oleracea*, *M. huberi*) (26.8%). For medium-sized seeds (*B. excelsa*, *C. guianensis*), we recorded 41 dispersal events (29.2%) and 19 predation events. For large seeds (*L. lurida*), we observed 28 dispersal events (13.6%) and one predation event (Figure 7).

We observed Squirrels (*Guerlinguetus* spp.) interacting only with two medium-seeded species, with a strong preference for *B. excelsa* (29 dispersal events; 14.4%), as indicated by a frequency nearly 15 times higher than interactions with *C. guianensis*. As expected, considering their arboreal habits,

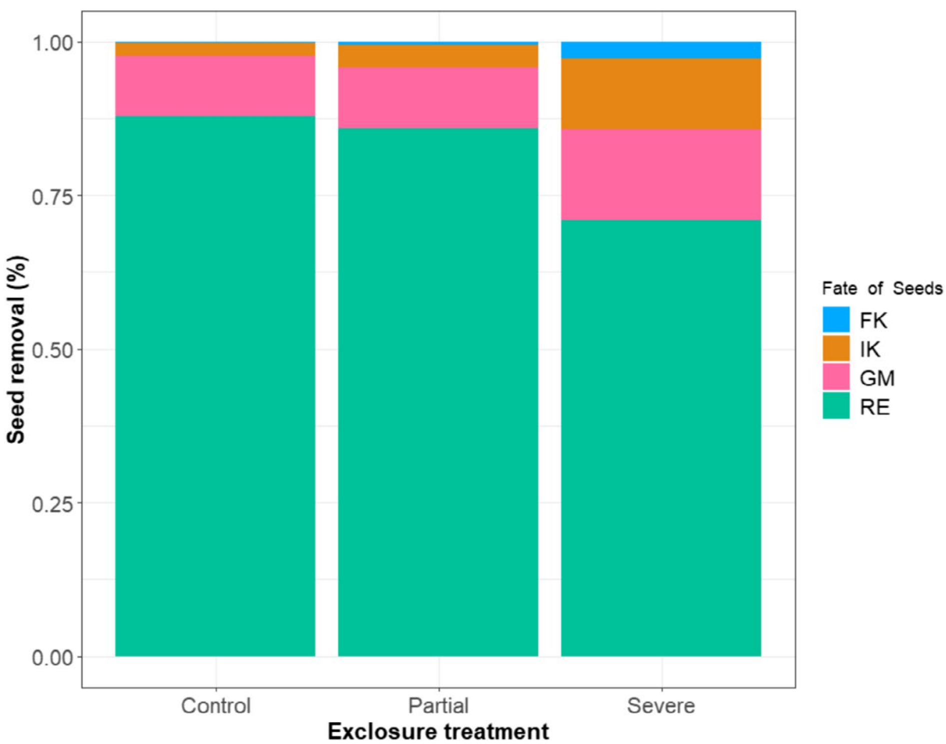

FIGURE 5 | Proportion of seed fates along the experimental gradient simulating defaunation (Control, Partial Exclusion, Severe Exclusion). Seeds were categorized as: Removed (RE), Invertebrate-Killed (IK), Fungal-Killed (FK), or Germinated (GM).

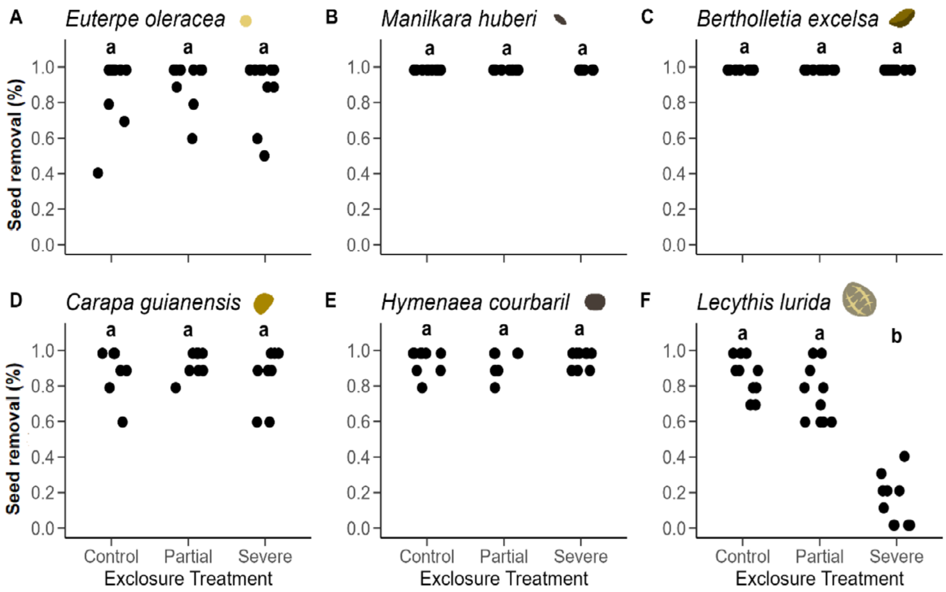

FIGURE 6 | Proportion of seeds removed by terrestrial mammals for each plant species across the experimental gradient simulating defaunation (Control, Partial Exclusion, Severe Exclusion). Black dots represent observed values per plot ($n=10$ per treatment). Identical letters indicate non-significant differences; different letters indicate significant differences.

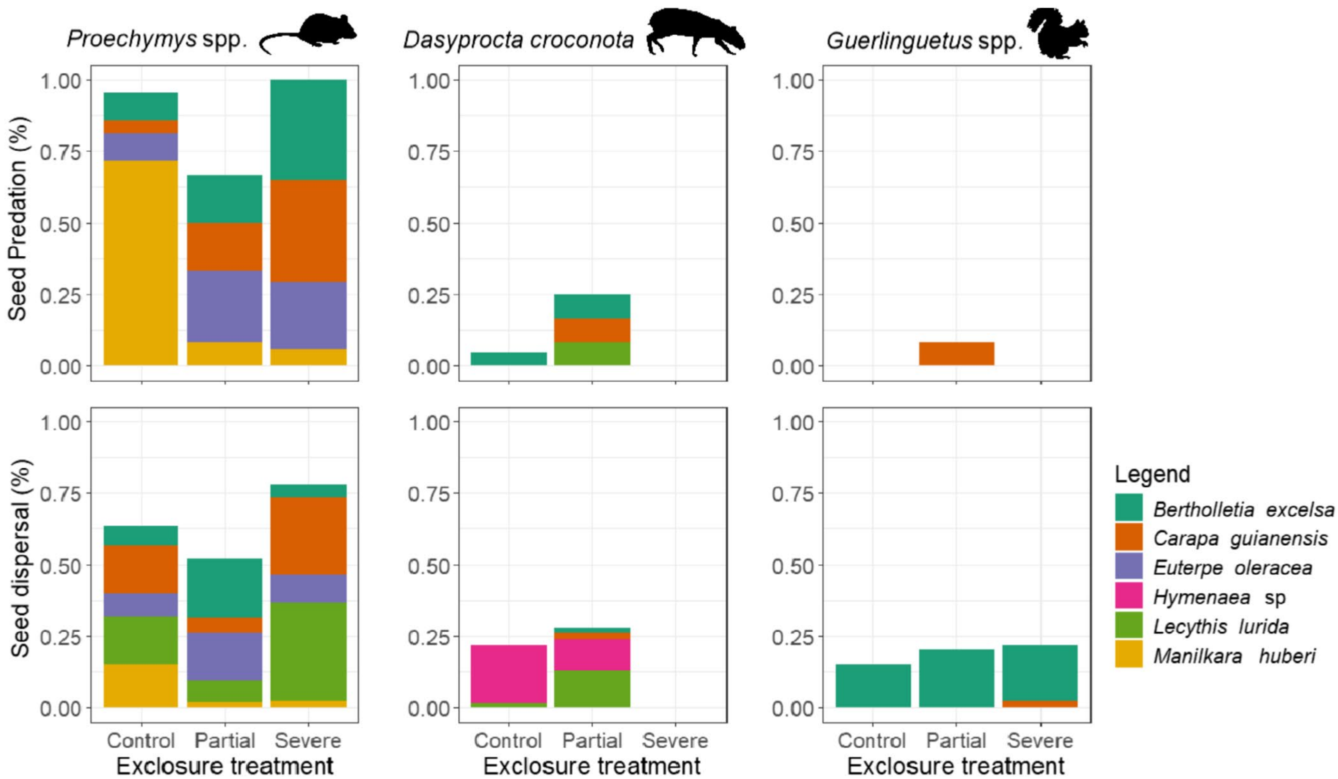

FIGURE 7 | Proportion of recorded dispersal and predation interactions between terrestrial mammals and seeds of different plant species along the experimental gradient simulating defaunation. (Control, Partial Exclusion, Severe Exclusion).

they showed no difference in interaction frequency between treatments.

Agoutis *D. croconota* also interacted with multiple species and showed generalist behavior, removing 28 seeds and preying upon four species, all from medium- to large-seeded species. However, agoutis were only able to interact with seeds in the control and partial exclusion plots. We note that in partial exclusion plots, we observed fewer *Proechimys* spp. interactions and more frequent interactions with *D. croconota* (Figure 7).

Among the recorded mammals, only *Proechimys* spp. had enough interaction records for statistical analysis testing differences among seeds of different sizes. Despite frequent interactions, we found no significant effect of defaunation on the frequency of *Proechimys* spp. interactions with seeds of different sizes: small ($\chi^2=3.732$; df=2; $p=0.154$), medium ($\chi^2=0.193$; df=2; $p=0.907$), and large ($\chi^2=0.000$; df=2; $p=1.000$). These results suggest that the presence or absence of medium- and large-bodied mammals did not significantly influence the behavior of this small rodent in seed handling across the defaunation gradient.

4 | Discussion

In this study, we used a terrestrial mammal exclusion experiment to simulate a defaunation gradient to assess, for the first time in the Amazon rainforest, the effects of defaunation on the early stages of recruitment in plant species of commercial interest. Our results support the hypothesis that the exclusion of medium- and large-bodied mammals significantly reduces seed removal, but only for larger seeds. The reduction observed in severe exclusion plots reinforces the central hypothesis of this study and aligns with patterns documented in tropical forests on other continents (Rosin and Poulsen 2016; Williams et al. 2021). These findings underscore the ecological importance of terrestrial mammals in plant regeneration dynamics, although the effects of defaunation may vary depending on the ecological context and the species involved (Galetti, Bovendorp, and Guevara 2015; Williams et al. 2021).

When examining each plant species individually, we found that defaunation did not significantly affect seed removal in five of the six species evaluated. The exception was *L. lurida*, whose seeds, the largest in our study, experience significantly reduced removal rates in severe exclusion plots. This result is consistent with studies showing that larger seeds depend more heavily on large-bodied mammals for removal and dispersal (De Mattia et al. 2006; Chen et al. 2021). Furthermore, when large vertebrates were experimentally absent, *L. lurida* seeds exhibited high rates of predation by invertebrates (66%) and attack by fungi (16%), suggesting that the absence of seed removal may substantially increase seed mortality (but see Cuny et al. 2022) that reported cases where insect predation can even increase plant germination. Similar results were reported by Williams et al. (2021), who demonstrated in a Bornean rainforest exclusion experiment that in the absence of removal by large vertebrates seeds were subjected to increased levels of seed predation by insects and fungi, maintaining high seed mortality rates. However, despite this functional compensation in mortality, it is important to note that while insects and fungi act primarily as predators of large seeds, vertebrates such as agoutis, in addition to frequently acting as predators, also have the potential to disperse larger seeds through removal and caching. This process allows plant establishment away from the source and influences the spatial distribution of plant populations (Jansen et al. 2012; Mittelman et al. 2020). Thus, even when mortality rates remain constant, the absence of vertebrates capable of removing and eventually dispersing large seeds can impair regenerative processes and affect long-term seedling recruitment dynamics for large-seeded plants.

Although more frequent in large-seeded species, partial compensation by invertebrates and fungi was a general pattern in severe exclusion plots, where invertebrate predation increased across several species. For instance, while combined mortality from fungi and invertebrates ranged from 2% to 14% in control and partial exclusion plots, it exceeded 30% for some species in the severe exclusion treatment. This reinforces the idea that the absence of vertebrates not only reduces potential seed dispersal but also leaves seeds more vulnerable to pathogenic and specialized herbivore attacks. These interactions are rarely considered in defaunation studies but may have direct effects on seed survival and forest regeneration (Williams et al. 2021; Rosin and Poulsen 2018). The intensification of post-dispersal mortality by these agents suggests that vertebrates play a broader ecological role—acting also as indirect modulators of biotic pressure on viable seeds.

Although our results highlight the importance of mammals in seed removal, we did not record interactions with large-bodied species such as tapirs (*T. terrestris*) and white-lipped peccaries (*T. pecari*) along the defaunation gradient. These mammals are widely recognized as key frugivores that can both predate and disperser seeds in tropical forests (Galetti, Bovendorp, and Guevara 2015; Peres et al. 2016; Fedriani et al. 2020), and their presence has been previously documented in our study area (Brocardo et al. 2023; Batista et al. 2025). However, the primary agents of seed removal in our experiment were small- and medium-bodied rodents, particularly *Proechimys* spp. We observed that in the absence of medium-sized rodents such as *D. croconota*, seed removal by smaller rodents increased considerably, suggesting a potential mechanism of functional compensation. Nonetheless, our observations also indicate that the ability of these small rodents to handle seeds may be constrained by seed size, as small and medium seeds were removed more frequently than large seeds, indicating possible physical limitations in handling and transporting heavier seeds (Dylewski et al. 2020; Meiga and Christianini 2020). These findings support the hypothesis of a potential trade-off between disperser body size and seed size (Dirzo and Mendoza 2007; Maron et al. 2018; Dylewski et al. 2020). Still, our statistical analyses did not detect significant differences in removal rates by *Proechimys* spp. across seed size classes, suggesting that other factors, such as seed coat texture, chemical composition, or position on the forest floor, may also influence disperser choice. Additionally, although small-sized rodents generally have lower movement capacity than larger rodents such as agoutis and pacas, many act primarily as seed predators rather than dispersers (Adler and Kestell 1998). They often lack behaviors such as caching or burying seeds, which enhance the chances of successful dispersal. Thus, even if small rodents quantitatively compensate for seed removal, it is unlikely that they provide qualitative benefits equivalent to those of larger mammals. Therefore, it is unrealistic to expect that a single trait can explain the complexity of plant–animal interactions or the dynamics of seed removal (Chen et al. 2021).

The combined use of camera traps and seed removal experiments also revealed behaviors rarely documented in previous studies, despite their important implications for recruitment limitation (Rosin and Poulsen 2016, 2018). For instance, *Proechimys* spp. was recorded consuming sprouts of *E. oleracea* and germinated seeds of *C. guianensis* (see Data S1), indicating that even germinated seeds may fail to reach the seedling stage due to post-germination herbivory. These findings highlight *Proechimys* spp. as the predominant species removing seeds throughout the experiment, except for *L. lurida* seeds. However, it is crucial to emphasize that *Proechimys* spp. is primarily a seed predator rather than a disperser (see Adler and Kestell 1998). Whereas *D. croconota* can contribute extensively to seed dispersal and consequently to the recruitment of a variety of plant species (Mittelman et al. 2021). Thus, the absence of *D. croconota* in areas with severe exclusions may have reduced the ratio between seeds dispersed and predated, with fewer seeds being dispersed and more seeds being preyed upon. This, in the long-term, may result in a decrease in the density and diversity of commercially important trees, which may have significant economic impacts on both traditional communities that depend on these species for their subsistence, as well as the timber industry, which relies on the exploitation of these tree species. Therefore, our findings support that considering the implications of defaunation is crucial for sustainable forest management and conservation of commercially important plant species.

Our findings contribute to a better understanding of the effects of defaunation on seed removal and fate which affect seed germination and seedling recruitment. We suggest that future studies experimentally manipulate access by different groups of seed removers under realistic seed availability conditions, incorporating a broader set of seed traits. This approach may help clarify how defaunation influences seed removal and fate, and how these effects vary with plant morphological, chemical, and functional characteristics (Williams et al. 2021; Chen et al. 2021).

Author Contributions

A.C., R.F. and M.P.: conceptualization; A.C., C.B.: data collection; A.C., C.R., R.F., C.B., I.W. and M.P.: writing – original draft preparation; A.C., C.R., R.F. and M.P.: writing – review and editing; A.C., C.R. and R.F.: visualization; C.R., R.F. and M.P.: supervision. All authors have read and agreed to the final version of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Figshare at https://figshare.com, reference number https://doi.org/10.6084/m9.figshare.31324600.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1–S2:** btp70183-sup-0001-Supinfo.docx.