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Received: 5 April 2024 | Revised: 21 August 2024 | Accepted: 23 August 2024

DOI: 10.1111/btp.13381

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ORIGINAL ARTICLE

Vertebrate seed predation can limit recruitment of later-successional species in tropical forest restoration

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Funding information
Directorate for Biological Sciences, Grant/Award Number: DEB 0515577, DEB 1456520 and DEB 2016623

Associate Editor: Jayashree Ratnam
Handling Editor: Kim McConkey

Abstract

The effects of vertebrate seed predation on the regeneration of restored forests are not well understood because most past studies have focused on seed predation within the first few years after restoration and have measured seed removal without quantifying subsequent seedling establishment of seeds that avoid predation. Quantifying the establishment of seeds that escape predation in restored forests at later stages of regrowth is crucial for anticipating longer-term recovery trajectories. Here, we evaluated the potential role of vertebrate seed predators in limiting recruitment of later-successional tree species in nine forests actively restored ≥15 years prior and in four paired remnant forest fragments embedded in an agricultural landscape in southern Costa Rica. We conducted seed addition experiments with four tree species inside and outside vertebrate exclosures and used camera trapping to detect seed predators. To determine the fate of seeds that avoided predation, we also measured seedling establishment after 1 year, given that other mortality factors may compensate in the absence of vertebrate seed predation. We detected two species of birds and five species of granivorous mammals removing seeds. Seed tagging indicated that most removal resulted in predation. For three of the four tree species tested, vertebrate seed predation reduced seedling establishment. The magnitude of this effect depended on species' susceptibility to other causes of mortality during the seed-to-seedling transition. Our study demonstrates that vertebrate seed predators can substantially reduce later-successional seedling recruitment in restored forests and should be considered alongside dispersal limitation and microsite conditions as factors slowing forest recovery.

Abstract in Spanish is available with online material.

KEYWORDS
Costa Rica, ecological restoration, exclosure experiment, seed addition, seedling establishment, succession, tree plantation

1 | INTRODUCTION

Vertebrate seed predation can play important roles in tropical forest dynamics by shaping spatial and temporal patterns of plant recruitment and the relative abundances of different species (Clark et al., 2012; Janzen, 1971; Paine et al., 2016; Rosin & Poulsen, 2016; Silman et al., 2003; Wright, 2003). Although post-dispersal seed predation by vertebrates is a natural ecosystem process long recognized to influence seedling community structure (Asquith et al., 1997; Orrock et al., 2006), it has the potential to slow forest recovery

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and is typically considered a barrier rather than a restoration target (Doust, 2011; Pearson et al., 2022).

Vertebrate seed predation could affect tree seedling recruitment differently in restoration plantings ("active restoration") compared to intact or remnant forests for multiple reasons. First, restoration sites (both passive and active) often lack reproductive individuals of many tree species during the initial years of succession (Caughlin et al., 2019; Van Breugel et al., 2007), so seed rain for many species is comprised primarily of immigrant seeds. Even in restored forests planted with native species, the trees require time to reproductively mature, and the diversity of planted species is typically much lower than that in remnant forests (de Almeida et al., 2024). This means that for later-successional tree species, especially larger-seed species which are more strongly dispersal-limited, most recruitment is from low-density immigrant seed rain, in the tails of seed shadows (de la Peña-Domene et al., 2013). In this scenario negative density-dependence resulting from natural enemies is expected to be weaker (Comita et al., 2014), so the relative importance of seed predation by generalist granivores may increase. Second, the faunal assemblages using restoration plantings are often distinct from those using remnant forests (Zagal-García et al., 2022), which may result from altered habitat structure and resources, small area, and isolation from source populations (Galetti et al., 2017; Ribeiro da Silva et al., 2015).

Despite these differences and their potential implications for tropical forest recovery, a recent meta-analysis found that seed predation was the least common plant–animal interaction examined in studies comparing restored and reference systems (Genes & Dirzo, 2022). Furthermore, many seed predation studies related to tropical forest recovery historically focused on seed predation as a barrier to initial recruitment in abandoned pasture (Holl & Lulow, 1997; Jones et al., 2003; Myster, 2003). But the role of vertebrate seed predation may change as succession proceeds (Yang et al., 2018). Better understanding the outcomes of seed predation interactions may be key to predicting and managing successional pathways at existing and future restoration sites to improve outcomes for biodiversity and carbon storage (Culot et al., 2017).

Identifying which vertebrate species are responsible for post-dispersal seed removal is necessary to understand if and how altered faunal assemblages at restoration sites influence the seed-to-seedling transition for immigrant seeds. For example, the absence of large-bodied animals at restoration sites could release large-seeded species from seed predation and increase seedling establishment, as has sometimes occurred in response to loss of large fauna (Dirzo et al., 2007; Mendoza & Dirzo, 2007; Silman et al., 2003). Alternatively, if extant smaller vertebrates or seed-eating insects are able to compensate for the absence of larger seed predators, different faunal communities could yield similar seed predation outcomes (Brewer et al., 1997; Rosin & Poulsen, 2018). It is also especially important to identify the vertebrates removing seeds because some species act as both seed predators and secondary dispersers (Gómez et al., 2019; Mittelman et al., 2021; Vander Wall et al., 2005).

Evaluating whether the effects of vertebrate seed predation carry through to seedling establishment is key to understanding its role in recruitment limitation. Many seed predation studies only examine seed removal over the short term (days to weeks) (Dylewski et al., 2020; Moles & Westoby, 2003), yet the remaining seeds are not guaranteed to complete the seed-to-seedling transition. So the importance of vertebrate seed predation for recruitment outcomes can be overestimated when other causes of mortality fully or partially compensate for the loss of vertebrate seed predators (Terborgh, 2013; Williams et al., 2021). Therefore, monitoring seed fates through the full seed-to-seedling transition provides a more realistic picture of vertebrate seed predation effects.

Here, we conducted a seed addition and vertebrate exclosure experiment in two habitat types (restoration plantings and remnant forest) using four large-seeded (>10-mm), animal-dispersed, later-successional tree species, within a long-term, well-replicated restoration experiment in southern Costa Rica. We paired the seed addition experiments with camera trapping to assess overall vertebrate use of habitats and link faunal communities to seed predation outcomes. We asked: (a) Which species are seed predators on larger seeds in this fragmented agricultural landscape? (b) To what degree does seed predation by granivorous mammals and birds reduce seedling recruitment? (c) Does seed predation, and its net effects on seedling establishment, vary between remnant forests and restoration plantings in their second decade of succession? We expected that experimentally added seeds would have higher survival when vertebrates were excluded and that rodents would be the main seed predators (Cole, 2009; Kuprewicz & García-Robledo, 2019). How closely seedling establishment success would match the proportion of seeds that avoided predation by vertebrates was an open question. Furthermore, we expected that the greater resource levels, habitat area, and structural complexity of remnant forests might result in greater activity of seed predators, but that high functional redundancy within faunal communities could result in similar seed predation rates between the two habitat types.

2 | METHODS

2.1 | Study area and long-term restoration experiment design

The study area is an agricultural landscape in southern Costa Rica (Coto Brus, Puntarenas Province). The region has a 3000-year record of human habitation, forest clearing, and agriculture (Clement & Horn, 2001), but the majority of the land is thought to have been forested until settlement by non-indigenous people in the mid-20th century, at which point land was rapidly deforested for conversion to agriculture (Zahawi et al., 2015). Remnant and secondary forest fragments are interspersed among pastures and row crops. The native ecosystem is transitional between premontane wet and rain forest (Holdridge et al., 1971). The study area receives ~3500–4000 mm

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annually, with a dry season from December to March, and has a mean annual temperature of ~21°C. Elevation of study sites ranges from ~1100 to 1200 m. The region hosts a high diversity of mammals (>100 spp.) (Pacheco et al., 2006) and birds (>400 spp.), although six species of large-bodied vertebrates have been locally extirpated (Daily et al., 2003). These include *Tapirus bairdii* (Baird's tapir) and *Tayassu pecari* (white-lipped peccary), a prominent seed predator in the Neotropics (Beck, 2005).

We conducted this study at nine sites (Figure 1, Table S1), a subset of the sites established in 2004–2006 as a long-term restoration experiment (Zahawi et al., 2013). Each site contains a 50 × 50 m plot (hereafter "restored forest") planted with two native timber tree species, *Terminalia amazonia* (Combretaceae) and *Vochysia guatemalensis* (Vochysiaceae), and two N-fixing species, *Erythrina poeppigiana* and *Inga edulis* (Fabaceae), with a consistent spacing of 2.8 m along the diagonal (Cole et al., 2010). Over the course of this study (January 2021–October 2023), restored forests ranged from 14 to 19 years old. Four of the nine sites had paired areas of remnant forest used as a reference for later-successional conditions in the region. Although nine sites were used overall, the number of restored forest sites used in seed addition experiments varied from six to eight, depending on species and experimental stage (seed removal or seedling establishment) because of the loss of one site to land use change (Table S1). The minimum distance between replicate sites was 0.7 km (median = 4.0 km, max = 7.8).

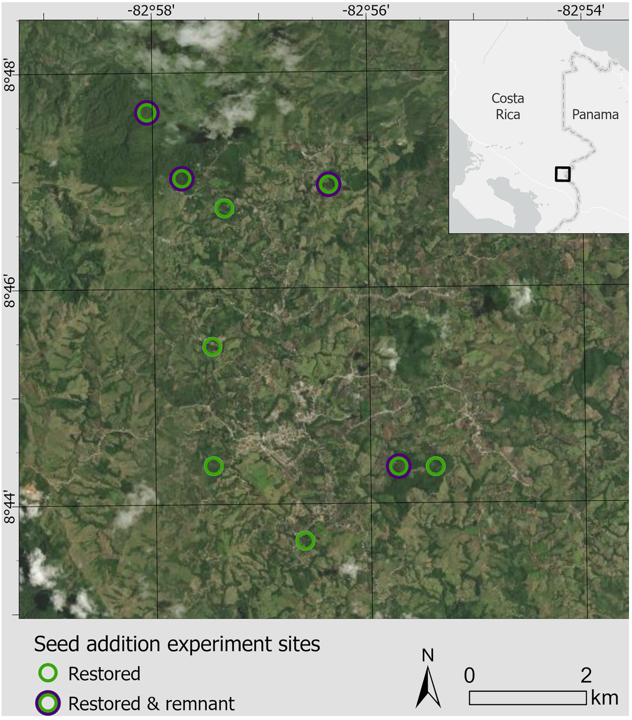

FIGURE 1 Map of study sites within Coto Brus, southern Costa Rica (8°45′34″N, 82°57′05.0″W). Green circles represent restoration sites. Green circles with purple outlines are sites with both a restored forest plot and a paired area of remnant forest.

2.2 | Baseline faunal surveys

To quantify habitat use by ground-dwelling mammals and birds and to identify the pool of potential seed predator species, we conducted camera trapping in restored and remnant forests. In January–June 2021, we deployed cameras at all sites except for one, which we surveyed in May 2022. Within each restored or remnant forest, we deployed two unbaited Bushnell Core DS cameras (models 119975C and 119977C; Bushnell, Kansas, USA), set to high sensitivity and programmed to capture five 8 MP images per trigger. To prevent disturbance to long-term research plots, we did not clear vegetation in front of cameras, and instead secured cameras to trees adjacent to suitable fields of view, but avoided aiming cameras at trails used by humans. The minimum distance between cameras was ~25 m. Our 50 cm deployment height is standard for monitoring mammals with camera traps (Kays et al., 2020), although consistently detecting and identifying small nocturnal mammals using camera traps is a common challenge (Gracanin et al., 2019). The duration of each camera deployment was ~55 days, but effective survey effort was lower for some deployments due to camera failures. Total survey effort was 1311 trap-nights (524 in remnant forests and 787 in restored forests).

2.3 | Focal tree species selection and seed collection

We used four focal tree species for seed addition experiments (Table 1), which we selected on the basis of (a) seed availability during the study period; (b) occurrence in late-successional forest within the study region and some degree of natural recruitment within the long-term restoration experiment (Werden et al., 2020); and (c) larger seed size (≥10 mm width, ≥1 g fresh mass). This size class corresponds to the approximate maximum diameter of seeds that smaller frugivorous birds in this system can swallow (Reid et al., 2021), and is similar to the 12-mm threshold used to define large seeds in the Atlantic Forest biome (Bello et al., 2015). Seed species included *Pseudolmedia mollis*, *Quercus benthamii*, and *Otoba novogranatensis*, and *Ocotea puberula* (hereafter referred to by generic names) collected from the ground under at least three mother trees per species. We manually removed pulp from *Pseudolmedia*, whereas birds had already removed pulp from most *Ocotea* and *Otoba* seeds. We measured fresh mass and width (minimum dimension) for a subsample of >50 seeds of each species. Before seed additions, we thoroughly mixed seeds to avoid plot-level bias in seed source or quality. We also briefly submerged all seeds in water to identify and remove insect-damaged or otherwise non-viable seeds (indicated by floating).

2.4 | Seed addition experimental design

In June 2021, we set up four stations within each 50 × 50 m restoration plot and each remnant forest fragment. In each restored forest

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TABLE 1 Focal tree species added in exclosure experiments.

Species (authority)	Family	Seed mass (g)	Seed width (mm)	Seeds per quadrat	Month collected	Removal survey period (weeks)
Ocotea puberula Nees	Lauraceae	1.1 ± 0.2	10 ± 1	7	August 2022	7
Otoba novogranatensis Moldenke	Myristicaceae	5.0 ± 1.4	20 ± 2	8	April 2022	8
Pseudolmedia mollis Standl.	Moraceae	5.7 ± 1.4	21 ± 2	11	June 2021	11
Quercus benthamii A. DC.	Fagaceae	10.1 ± 2.6	25 ± 2	7	July 2021	8

Note: Measurements are means (±1 SD) from a sample of >50 seeds per species.

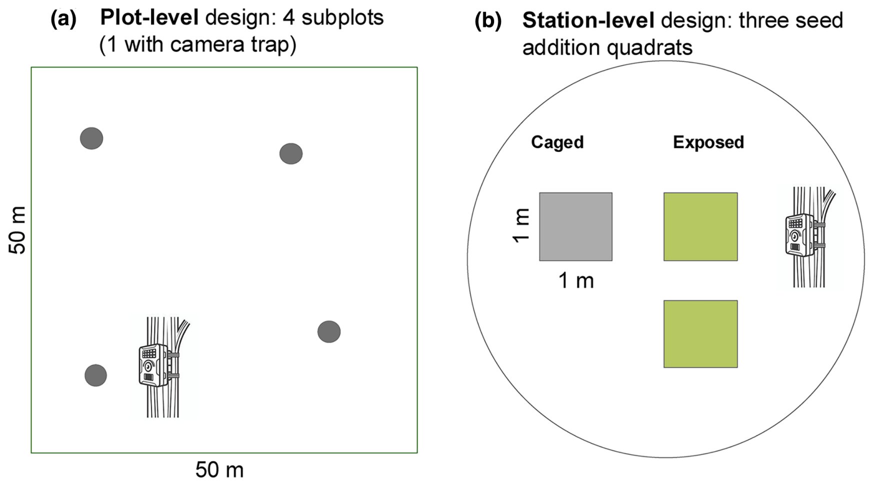

FIGURE 2 Experimental design showing (a) plot-level design with one station distributed in each quadrant of each 50 × 50 m restored forest plot and similarly distributed within remnant forest patches (not pictured); and (b) station containing one seed addition quadrat with a 0.3-m tall vertebrate exclosure (represented by a gray square) and two exposed seed addition quadrats (green squares). At one station per plot, a camera trap was positioned to detect vertebrates encountering experimental seeds in exposed quadrats.

plot, one station was distributed in each quarter of the plot (Figure 2). The minimum distance between stations was ~15 m. We installed one exclosure (1 × 1 (wide) × 0.3 (tall) m rebar frame secured to the ground and covered with 1.27 cm wire mesh) in each station and demarcated two adjacent 1 × 1 m seed addition quadrats that were exposed to vertebrate seed predators (Figure 2). Previous research in this region found that this mesh size was sufficient to exclude small mice (Holl & Lulow, 1997). We marked the corners of exposed quadrats with stake flags and secured a roll of fine mesh ~5 cm high on the downhill side to catch any seeds washed downslope by runoff. We did not remove natural vegetation from seed addition quadrats, since vegetation removal could have increased detectability by predators and also affected subsequent seedling establishment.

We sequentially added seeds of the four focal tree species in July 2021, April 2022, and August 2022 (Table 1). We placed seeds directly on top of the litter layer or soil surface to simulate how seeds would naturally be deposited by primary dispersal, pressing down slightly to prevent seeds from rolling away on steeper slopes. Seeds were distributed systematically following a predetermined grid configuration with 10–20 cm minimum spacing.

We censused all quadrats at ~7–11 weeks post-addition to count the number of seeds remaining ($n = 3024$ seeds added). We also quantified vertebrate-seed encounters for each species in one exposed quadrat per plot by deploying a camera trap 1.5–2 m above the ground, with the entire seed quadrat in the field of view. Camera traps were deployed for the initial ~7 weeks after seeds were set out, with individual camera deployment durations (range 7–51 days) depending on seed species, camera functioning, and whether all seeds had already been removed.

We also censused seedling establishment ($n = 2880$ seeds) for each species after 1 year (12–15 months). When monitoring quadrats, we scattered any leaf litter accumulated on the top or sides of an exclosure inside that cage to reduce shading and litter depletion effects. Because seed additions were staggered by species, the intervals between monitoring visits varied from 1 to 5 months. Litter depth was slightly reduced within exclosures compared to open seed addition quadrats, from 2.7 ± 0.8 to 1.9 ± 1.1 cm (mean ± SD, $p < .001$, Figure S2). There was no evidence that this effect differed between forest types ($p = .20$), nor was there a difference in overall litter depth between forest types ($p = .19$, Table S2).

2.5 | Seed tagging

To assess the degree to which seed removal might represent seed dispersal by scatter-hoarding rodents, rather than seed predation, in July–August 2022 we conducted a follow-up seed-tagging experiment at two of the sites that had paired remnant forest and had previously shown high levels of seed removal. We sequentially quantified secondary dispersal for two of the previously added species. In each plot, we set up five stations. First, we glued 50-cm lengths of pink nylon string with labeled flagging to *Pseudolmedia*

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seeds and placed 10 seeds (eight tagged, two non-tagged) in each station, spaced 20 cm apart, with leaf litter covering the string and flagging so that only the seeds themselves were exposed. We monitored two of the five stations in each plot using camera traps positioned as previously described. We checked stations weekly for 6 weeks, assessing in situ seed fate and searching the area surrounding each station for dispersed seeds. We searched for missing seeds at each station for ~5 min, starting within 5 m of the original location and expanding the search radius up to ~15 m as needed. We marked the location of each scatter-hoarded seed with a bamboo skewer and re-checked their location and predation status weekly until the seed was predated or the end of the tagging experiment, whichever occurred first. Then, we repeated the process for *Quercus* with four seeds per station and monitored the seeds for 3 weeks. Since we had not observed an effect of tagging on *Pseudolmedia* removal rates, we tagged all four *Quercus* seeds.

2.6 | Data analysis

We processed camera trap images in *camelot* software (Hendry & Mann, 2017) and calculated a relative activity index (RAI, independent detections per 1000 trap nights) for each species in both habitat types. We used 30 min as the threshold for independent detections (Burton et al., 2015). Because detectability varies by species and habitat, this index is not a reliable proxy for abundance (Sollmann et al., 2013), but at a minimum, this approach documents species presence within the two habitat types and provides initial insights into coarse-level activity patterns. Small nocturnal rodents (families Muridae, Heteromyidae, and Echimyidae) were not identifiable in camera trap images and thus binned into a single "unidentified mouse/rat" category.

Camera trap monitoring of exposed seed addition quadrats sometimes provided clear evidence of seed removal or consumption, but we were not consistently able to attribute the removal of each individual seed to a particular interaction or even vertebrate species. Instead, we quantified independent detections of granivorous species encountering seed addition quadrats. We used the package *bipartite* to visualize bipartite networks of vertebrate-seed encounters between experimental seeds and the granivorous vertebrates confirmed to consume at least one focal species, aggregated by forest type (restored or remnant forest). These networks visualize overall exposure of experimental seed quadrats to granivores but cannot be interpreted as a robust quantification of interaction strength.

To test for the main effects of vertebrate exclosures and forest type, as well as their interaction, on the proportion of seeds remaining and the proportion of seeds established as seedlings after 1 year, we fit binomial generalized linear mixed models (GLMMs) using package *lme4* v 1.1. For each response variable, we fit an overall model with species and station within site as random predictors. We also explored species-specific effects by modeling response variables for species individually, although this was not possible for all species × response variable combinations because some models failed to converge. For post-hoc comparisons, we obtained estimated marginal means using package *emmeans* v. 1.8.1. All analyses were conducted in R v.4.2.1 (R Core Team 2022).

3 | RESULTS

3.1 | Faunal surveys

Camera trap surveys in restored forest plots and remnant forests prior to seed addition experiments detected 21 mammal taxa and 41 bird taxa (Table S3), 17 of which are granivorous. The three most frequently detected granivore species were *Dasyprocta punctata* (Central American agouti, Figure S1a), *Leptotila cassinii* (gray-chested dove), and *Odontophorus gujanensis* (marbled wood-quail, Figure S1b), which collectively accounted for 36% of independent mammal and bird detections.

Camera trapping in seed quadrats detected two bird species and at least five mammal species consuming or removing experimental seeds (Table 2, Figure 3, Table S3). Great tinamous (*Timanus major*) have sufficiently wide bills to swallow large seeds. Marbled wood-quail (*O. gujanensis*), in contrast, were observed pecking at seeds and eating the fragments. Smaller granivorous birds such as doves (*Leptotila*, *Geotrygon*) and sparrows (*Arremon* spp.) were never detected interacting with added seeds.

Some granivore species that consumed large seeds were more frequently detected in remnant than restored forests in both rounds of camera trapping (Table 2, Figure 3). For example, agouti (*D. punctata*) detections were more than 10 times as frequent in remnant forests as in restored forests. Furthermore, two species, *O. gujanensis* and *Dicotyles tajacu* (collared peccary, Figure S1c), were only detected at the two sites embedded within the largest forest fragment in the landscape.

The relative frequency of mouse/rat encounters with seed addition quadrats was higher in restored forests (Figure 3), although this was driven by high numbers of detections in particular quadrats that presumably overlapped with the small home ranges of mice/rats that were detected repeatedly. In most cases, mice/rats were not observed removing experimental seeds.

3.2 | Seed removal

Overall, vertebrate seed predators strongly reduced the proportion of seeds remaining in exposed quadrats ($z = -14.32$, $p < .001$, Figure 3a, Table S4); the percentage (mean ± 1 SD) of seeds remaining at 7–11 weeks in exposed quadrats was 50.8 ± 5.2%, compared to 94.4 ± 1.6% in exclosure quadrats. In some cases (especially for *Ocotea*), the percentage of seeds remaining in caged quadrats was lower than 100%, but these seeds likely were not found due to burial under shifting litter or because they died and rotted before they were censused. The proportion of seeds remaining was slightly but significantly lower in restored than in remnant forests both inside and outside exclosures ($z = -2.90$, $p = .003$, Table S4).

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TABLE 2 Vertebrate seed predators detected removing seeds.

Taxon	Common name	Possible seed disperser	Rest. RAI	Rem. RAI
Birds				
Odontophorus gujanensis	Marbled wood-quail	No	5.1	105.0
Tinamus major	Great tinamou	No	34.3	36.3
Mammals				
Cuniculus paca	Tepezcuintle	No	8.9	43.9
Dasyprocta punctata	Central American agouti	Yes	72.4	814.9
Sciurus granatensis	Red-tailed squirrel	Yes	24.1	36.3
-------	Unidentified mice/rats	Yes[a]	38.1	43.9
Dicotyles tajacu	Collared peccary	No	0	7.6

Note: We determined the status of each species as a potential seed disperser based on the literature. The relative activity index presented for restored (Rest.) forests and remnant (Rem) forests is based on the number of independent detections per 1000 trap nights across all sites of each habitat type.

[a] To our knowledge, *Heteromys desmarestianus* is the only known scatterhoarding species of the 14 species of mice and rats documented in the region.

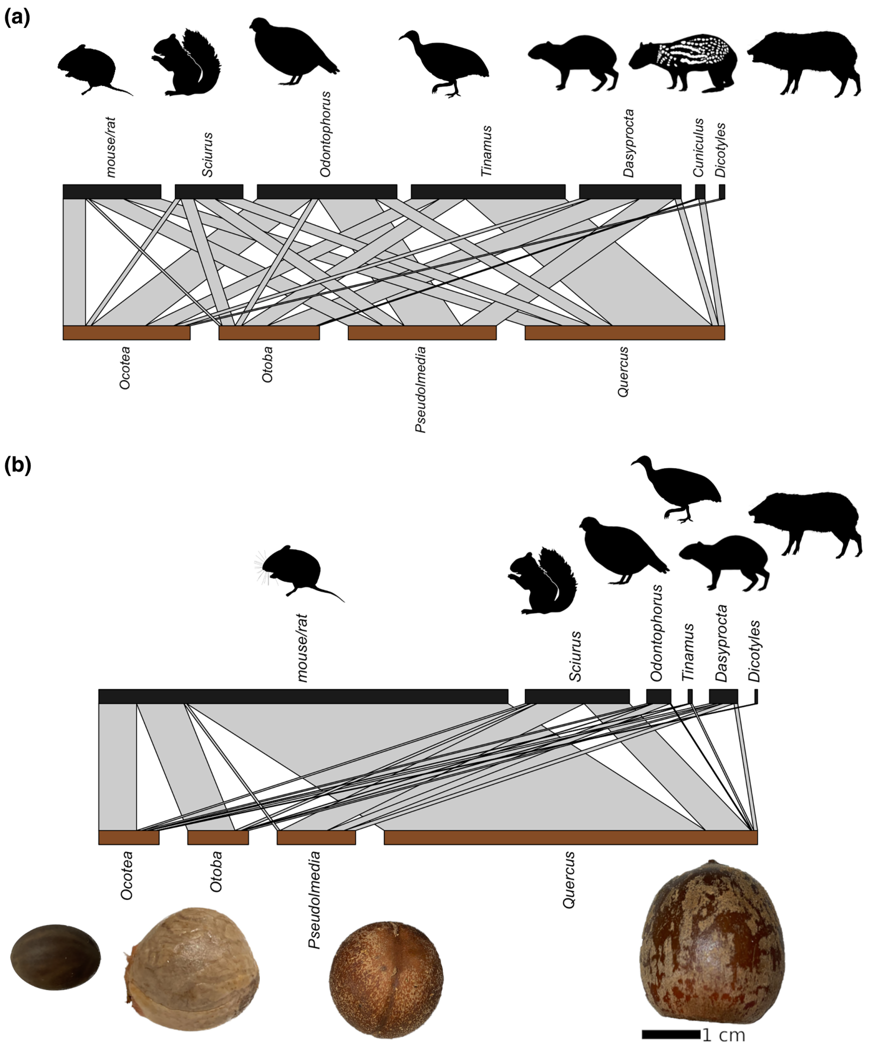

FIGURE 3 Bipartite networks depicting vertebrate-seed encounters detected by camera trapping of seed addition experiments in (a) remnant forest and (b) restored forests. Note that each encounter between a confirmed seed predator species and seed addition quadrat does not necessarily represent an individual seed predation event. Species are ordered from left to right by increasing mass (vertebrates not to scale). For full species names, see Table 1 (trees) and Table S1 (vertebrates). Vertebrate silhouettes from PhyloPic (phylopic.org).

Differences in census timing preclude direct comparisons among species, but we observed highest removal for *Pseudolmedia*, intermediate removal for *Quercus* and *Ocotea*, and lowest removal for *Otoba* (Figure 3a).

3.3 | Seed tagging

Most (78%) of *Pseudolmedia* and *Quercus* seeds removed by vertebrates in the seed-tagging study were consumed within a 2-m radius

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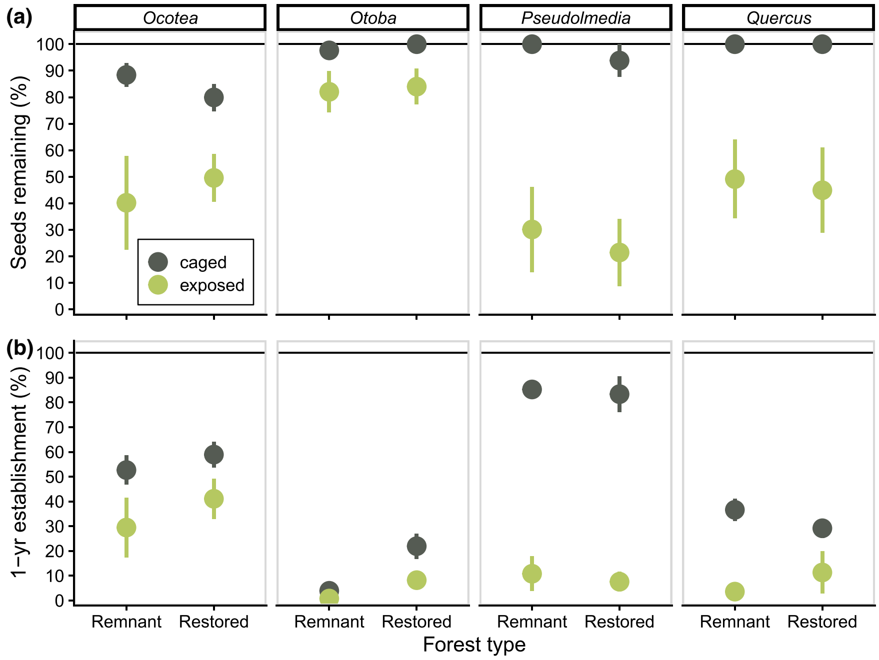

FIGURE 4 Percentage of (a) seeds remaining (i.e., not removed) 7–11 weeks post-addition and (b) added seeds established as seedlings after 1 year, for all species, forest types, and exclosure treatments. Points represent treatment means of plots (averaged over four stations) and lines represent 1 SE. $N = 6–8$ restored forests, depending on response variable and species; $n = 4$ remnant forests for all species.

of their original position, as indicated by seed fragments or strings with no seed attached. Weekly monitoring and camera trap images revealed that 18 seeds (9% of *Pseudolmedia* seeds) were scatter-hoarded (secondarily dispersed) by agoutis (*D. punctata*) within 5 m of the station. These dispersal events were only observed for *Pseudolmedia* and within remnant forest. Sometimes a seed was repeatedly moved and recached, but the majority of scatter-hoarded seeds (10 of 18) were eventually consumed within the 6-week experiment.

3.4 | Seedling establishment

Seedling establishment after 1 year was significantly greater inside exclosures compared to exposed quadrats ($z = -15.76$, $p < .001$, Table S5); 46.3 ± 4.3% of added seeds established in exclosures and 15.6 ± 3.1% of added seeds established in exposed quadrats (Figure 4b). The probability of a caged seed establishing was not different between restored and remnant forests ($z = -0.7$, $p = .48$), but exposed seeds were significantly less likely to establish in remnant forest ($p = .038$, Table S5). This was driven by *Quercus*, which was less likely to establish as a seedling in remnant forest ($p = .01$, Table S6). In contrast, only caged *Otoba* seeds were less likely to establish as seedlings in remnant forest, whereas for *Ocotea* and *Pseudolmedia* there was no significant interaction between exclosure treatment and forest type on establishment success.

4 | DISCUSSION

Our use of exclosures, camera trapping, and seed tagging provided direct evidence that vertebrate seed predation reduced seed survival (Figure 4a), consistent with shorter-term studies in restoration and secondary forest contexts (Holl & Lulow, 1997; Peña-Claros & de Boo, 2002). By monitoring seed addition quadrats for a full year, we further showed that these initial effects translated to differences in seedling establishment (Figure 4b), although exclosure effects on establishment were smaller than their effects on removal and varied by species. Seedling establishment both inside and outside of exclosures was much lower than the proportion of non-removed seeds for all species except *Pseudolmedia*, indicating other mortality factors that varied by species. Encouragingly, in our study seed predation did not consistently result in lower seedling establishment at restoration sites compared to remnant forests, unlike the pattern of herbivory effects on vegetation recovery documented in a recent global meta-analysis (Xu et al., 2023).

Although we did not quantify all mortality factors throughout the seed-to-seedling transition, we offer some context for species variation in patterns of seed removal, seedling establishment, and their correspondence. Variation in time to germination means that caution is warranted when comparing among species (Chen et al., 2021; Martin & Hargreaves, 2023), but we do not believe that the qualitative patterns observed were strongly confounded by exposure time. We observed high *Otoba* and *Quercus* seed mortality from predation by beetles (consistent with Santamaría-Aguilar & Lagomarsino, 2021) but were unable to quantify these effects without destructive sampling of seeds. Although vertebrate seed predation reduced seedling establishment for experimentally added *Quercus* seeds, it is worth noting that acorns of this species would be unlikely to arrive at restoration sites in the absence of scatter-hoarding by vertebrates, even if most interactions with mammals result in seed death. Many remaining *Ocotea* seeds germinated but suffered moderate mortality as seedlings. In contrast, *Pseudolmedia*

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showed very low mortality within exclosures and thus the strongest effects of vertebrate seed predation. Moreover, it also had long time to germination (>6 months in some cases), suggesting that levels of seed removal at 11 weeks underestimated total seed predation effects.

A varied assemblage of vertebrate seed predators encountered and consumed our focal seeds, although composition varied by site and habitat type. Agoutis were important seed predators but were only present at a subset of sites and showed greater activity in remnant forest. In contrast to reports of increased seed predation by small rodents in defaunated and fragmented landscapes elsewhere in the tropics (Galetti et al., 2015; Krishnan et al., 2022; Rosin & Poulsen, 2016), we rarely detected mice and rats removing seeds, despite their high levels of activity in restored forests. Red-tailed squirrels (*Sciurus granatensis*) also occurred in restoration plantings and were detected removing seeds more frequently than mice/rats. Marbled wood-quail (*O. gujanensis*) were unexpectedly frequent seed predators within the largest forest fragment. Although we are not aware of any studies documenting the seed predation interactions of *O. gujanensis*, the similar congener *O. capoeira* has been documented to eat large (>8-mm diameter) seeds in the Atlantic Forest (Galetti et al., 2015). As suggested by Pizo and Vieira (2004), granivorous birds may be important post-dispersal seed predators in some contexts (Christianini & Galetti, 2007; Palmer & Catterall, 2018) with effects comparable to mammals. Post-dispersal seed removal is not always a reliable proxy for seed predation (Vander Wall et al., 2005), and we detected two species known to effectively disperse seeds by scatterhoarding (*D. punctata* and *Sciurus novogranatensis*), but the results of our tagging experiment suggest that most seed removal observed in our study resulted in predation.

Although the exclosure treatment affected several variables that could have influenced seedling establishment, in addition to their intended effect of excluding vertebrates, these are unlikely to change overall conclusions. First, exclosures reduced the amount of litter, although on average there was still almost 2 cm of litter in exclosures. Since deeper litter can benefit larger-seeded species (e.g., through reduced desiccation, Muscarella et al., 2013; Sayer, 2006), if this difference biased seed and seedling survival at all, it likely would have caused us to underestimate rather than overestimate the benefits of vertebrate exclusion. Likewise, additional shading from litter on top of exclosure cages might have reduced the positive effects of exclusion on seedling establishment, even though focal species are generally shade tolerant. It is possible that shading could have increased mortality from phytopathogens favored by humid conditions (Milici et al., 2020). Second, exclosures protected seedlings from physical damage, for example from branch fall and trampling, that they would otherwise be subjected to (Clark & Clark, 1989) which would overestimate the positive effects of exclosures on seedling establishment. Based on an artificial seedling experiment at these sites (Quirós et al., in review), over a 1-year period ~13% of seedlings in remnant forests and ~18% of seedlings in restored forests would be expected to suffer physical damage though not necessarily fatal. These probabilities are unlikely to explain the magnitude of observed differences between caged and exposed establishment. Finally, the vertebrate exclosures could have also excluded some insect herbivores (e.g., lepidopterans laying eggs, large orthopterans), although they remained accessible to smaller insect herbivores (e.g., we observed leaf-cutting ants and herbivory inside exclosures). As such, some portion of the positive effects of exclosures may have been due to protection from insect herbivory, which reduces seedling survival (see Kulikowski et al. 2022).

Together, our results suggest that at sites with relatively low seed rain, recruitment of larger-seeded later-successional species could be further limited by high levels of seed predation, although other abiotic or biotic factors besides vertebrate seed predation substantially limit seedling establishment of most species in the first year. There have been recent suggestions for managing herbivores in successional contexts to reduce effects on vegetation diversity and abundance, for example by reintroducing carnivores (Huanca-Nuñez et al., 2023; Xu et al., 2023). However, neither reintroducing predators nor excluding seed predators is likely to be practical when (a) restoration sites are small and embedded within a fragmented landscape, and (b) vertebrate seed predator assemblages are comprised of species with diverse sizes and life histories. Direct seeding later-successional species has been suggested as a way to diversity depauperate secondary forests (e.g., Bonilla-Moheno & Holl, 2010) and restoration plantings (Sangsupan et al., 2018). Seed predation trials could help restoration practitioners to select tree species that are most likely to survive predation for broadcast sowing efforts.

AUTHOR CONTRIBUTIONS

Francis H. Joyce, Karen D. Holl, and Rakan A. Zahawi conceptualized the study. Francis H. Joyce and Brianna M. Ramos collected the data. Francis H. Joyce conducted analyses and wrote the first draft. All authors reviewed and edited the manuscript.

ACKNOWLEDGMENTS

We thank Gerald Quirós, Christian Benavides, Juan Abel Rosales, Jeison Rosales Umaña, Kassandra Navarro, Vanessa Morales, An Bui, Christina Blebea, Emanuel Pineda, Richard Joyce, and Maina Handmaker for assistance in the field. Maya Lara, Selma Ruiz, Karla Vaca, and Zachary Webster assisted with image processing. Brook Constantz helped create the site map. We thank Rebecca Cole for use of facilities at Loma Linda Field Station and Román Gómez for assistance with seed collection. Andy Kulikowski provided valuable advice and exclosure frame materials. Funding was provided by NSF (DEB 14-56520 and DEB 20-16623), American Philosophical Society, ARCS Foundation, UC Santa Cruz (Building Belonging Program, Environmental Studies Department). B. Ramos received funding from the Research and Extension Experiences for Undergraduates Program (grant no. 2016-67032-24987/project accession no. 1009021) from the USDA National Institute of Food and Agriculture. This research was approved by the UCSC Institutional Animal Care and Use Committee (#Hollk2104) and permitted by the Costa Rican Ministry of Environment and Energy.

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CONFLICT OF INTEREST STATEMENT

No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Dryad Digital Repository. http://doi.org/10.5061/dryad.05qfttfb9.

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SUPPORTING INFORMATION

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How to cite this article: Joyce, F. H., Ramos, B. M., Zahawi, R. A., & Holl, K. D. (2024). Vertebrate seed predation can limit recruitment of later-successional species in tropical forest restoration. *Biotropica*, *56*, e13381. https://doi.org/10.1111/btp.13381

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