

RESEARCH ARTICLE

Effects of large mammal exclusion on seedling communities depend on plant species traits and landscape protection in human-modified Costa Rican forests

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Abstract

1. Large terrestrial herbivorous mammals (LTH-mammals) influence plant community structure by affecting seedling establishment in mature tropical forests. Many of these LTH-mammals frequent secondary forests, but their effects on seedling establishment in them are understudied, hindering our understanding of how LTH-mammals influence forest regeneration in human-modified landscapes.
2. We tested the hypothesis that the strength of LTH-mammals' effects on seedling establishment depends on landscape protection, forest successional stage and plant species' traits using a manipulative field experiment in six 1-ha sites with varying successional age and landscape protection. In each site, we established 40 seedling plot-pairs, with one plot excluding LTH-mammals and one not, and monitored seedlings of 116 woody species for 26 months.
3. We found significant effects of LTH-mammal exclusion on seedling survival contingent upon the protection of forests at the landscape level and forest stage. After 26 months, survival differences between LTH-mammal exclusion and non-exclusion treatments were greater in protected than unprotected landscapes. Additionally, plant species' traits were related to the LTH-mammals' differential effects, as LTH-mammals reduced the survival of seedlings of larger-seeded species the most. Overall, LTH-mammals' effects translated into significant shifts in community composition as seedling communities inside and outside the exclosures diverged. Moreover, lower density and higher species diversity were found as early as 12 and 18 months outside than inside exclosures.
4. *Synthesis and applications.* Insight into the interactions between LTH-mammals and seedling communities in forest regeneration can be instrumental in planning effective restoration efforts. We highlight the importance of landscape protection in seedling survival and the role of LTH-mammals in promoting seedling diversity in mature forests but also in secondary successional forests. The findings suggest that conservation efforts and possibly trophic rewilding can be important approaches for preserving diversity and influencing the trajectory of secondary

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tropical forest succession. However, we also caution that an overabundance of LTH-mammals may adversely impact the pace of forest succession due to their preference for large-seeded species. Therefore, a comprehensive wildlife management plan is indispensable. Additionally, longer term studies on LTH-mammals are necessary to understand the effects of temporal fluctuations that are undetected in short-term studies.

KEYWORDS

community assembly, exclosure experiment, forest regeneration, herbivores, hunting protection, peccaries, secondary forests

1 | INTRODUCTION

Tropical forest landscapes are becoming increasingly fragmented and disturbed by land-use change, and as a result, secondary forests are growing in area and importance (Food and Agriculture Organization (FAO), 2020). Simultaneously, wildlife populations, including mammalian herbivores and granivores that interact with plants, are also being affected by anthropogenic changes in complex ways (Benitez-Malvido & Martinez-Ramos, 2003; Chazdon, 2014; Luskin et al., 2021). For example, while hunting for bushmeat can depress wildlife populations (Gallego-Zamorano et al., 2020), some herbivores and granivores populations are increasing where top carnivore populations have declined, with cascading effects on plant communities (Estes, 1996; Galetti et al., 2021; Jia et al., 2018; Terborgh et al., 2008) including many secondary forests' plant communities depending on their degree of landscape protection (i.e. hunting). Yet, the specific impacts within secondary forests remain less explored (DeMattia et al., 2006; Souza et al., 2022; Villar & Medici, 2021). This is partly because much of the focus on forest succession (e.g. Dupuy & Chazdon, 2008; Guariguata et al., 1997; Norden et al., 2017) has been on how changing availability of abiotic resources (e.g. light) affect succession, with less emphasis on the effects of biotic interactions, such as plant-animal interactions. Consequently, we do not have an ecologically comprehensive understanding of the mechanism driving changes in tropical forests' structure during secondary forest succession (Arroyo-Rodríguez et al., 2017).

Many plant-animal interactions are important for seedling establishment, but large terrestrial herbivorous and granivorous mammals (hereafter, LTH-mammals) are especially influential, as seeds and young seedlings (e.g. <20 cm tall) are particularly susceptible to herbivory (trophic) or trampling (non-trophic) (Dirzo et al., 2014; Ickes & Thomas, 2003). In tropical forests, LTH-mammals are recognized as an important biotic factor structuring seedling communities (Almeida-Neto et al., 2008; Beck et al., 2013; Clark et al., 2012; Kuprewicz, 2013; Luskin et al., 2021; Terborgh & Wright, 1994; Theimer et al., 2011). Some of these studies have found that LTH-mammals' effects on seedling establishment vary in strength (Kurten & Carson, 2015) among tree species. For example, foraging behaviour research showed that LTH-mammals prefer larger seeds (Forget & Jansen, 2007; Jansen et al., 2004; Martínez-Ramos et al., 2016) and

certain species such as palms or those with high lipid content (Akkawi et al., 2020; Beck, 2006; Villar et al., 2021). In addition, studies using exclosures to quantify the impact of mammals on plant communities found that the exclusion of LTH-mammals can increase seedling survival and density (Camargo-Sanabria et al., 2015; Kuprewicz, 2013; Murphy & Comita, 2020; Terborgh et al., 2008), change community composition, and increase seedling diversity (Dirzo & Miranda, 1990; Terborgh et al., 2008). In other studies, LTH-mammals strongly influenced density but not seedling richness (Beck et al., 2013; Paine & Beck, 2007; Theimer et al., 2011). However, these studies largely focus on mature forests, and our understanding of LTH-mammals' role in affecting seedling establishment in secondary forests is much less developed. Thus, our research aims to contribute to filling this important gap, particularly focusing on the role of LTH-mammals in seedling establishment in mature and secondary forests under both protected and unprotected landscapes.

In tropical forests, anthropogenic disturbances in various forms can complicate the relationship between landscape forest protection and LTH-mammal populations, making it context-specific. However, protected landscapes (i.e. no anthropogenic disturbances such as hunting or deforestation) generally tend to have a higher presence of LTH-mammals than unprotected ones with effects on plant communities (Dirzo & Miranda, 1990; Terborgh et al., 2008). The extent of these effects can hinge on plant species' traits, such as seed size, which can influence both the foraging behaviour of mammals and plants' shade tolerance (Martínez-Ramos et al., 2016). For instance, if the strength of the effect of LTH-mammals on seedling establishment varies among woody species, particularly when they preferentially consume hyperabundant seed-producing species or those with large seeds, then the trajectory of regeneration and, ultimately, the structure and composition of forest communities will shift. This outcome is particularly important in secondary forests, where the frequency of regeneration of woody species with different successional niches affects the trajectory of forest succession (Chazdon et al., 2007). Because forest regeneration in previously deforested areas depends critically on the survival and growth of early plant stages (Chazdon, 2014), insight into the interactions among LTH-mammals and young seedlings is essential for understanding how forests regenerate in increasingly anthropogenically modified landscapes.

This study investigates LTH-mammals' effects on seedling establishment and community structure of mature and secondary Costa Rican wet tropical forests. We tested the overarching hypothesis that the strength of LTH-mammals' effects on seedling establishment depends on species traits, forest successional stage (as mature and secondary forests), and landscape protection. Using six 1-ha forest sites, four secondary forests differing in successional age, and two mature forests, we established 40 pairs of seedling plots within sites that excluded or did not exclude LTH-mammals. We used two secondary and one mature forest site for each level of landscape protection (protected versus unprotected) to answer the following questions: (1) How does exclusion of LTH-mammals affect seedling survival in protected and unprotected landscapes for both mature and secondary forests? (2) Do the effects of LTH-mammal exclusion on survival vary among species of different traits? (3) Does LTH-mammal exclusion lead to shifts in the seedling community structure with time? We quantified seedling community structure based on stem abundance, rarefied species richness, evenness, and species composition and assessed the species traits based on their shade tolerance and seed size. If LTH-mammals exhibit differential effects among species and prefer larger-seeded and hyperabundant seed-producing species, we predict that LTH-mammals' exclusion would have a greater influence on seedling composition in protected and older forests. Also, the cumulative effects of LTH-mammal exclusion will consequently promote the dominance of abundant woody species, resulting in lower species richness and diversity inside than outside exclosures.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted in the tropical wet forest of La Selva Biological Station (hereafter, La Selva) and its surrounding areas in Sarapiquí province, Costa Rica. Permission to conduct the research in the area was granted by the Organization for Tropical Studies (OTS) and local landowners. Mean annual rainfall and temperature are ~4000 mm and ~26.5 °C, respectively. Given the shared regional tree species pool, the areas surrounding La Selva once contained forests with likely similar tree species composition but have experienced significant deforestation during the past 50 years (McClearn et al., 2016).

This study involves two 1-ha forest inventory sites (50 m × 200 m) established in secondary successional forests in 1997 and four 1-ha sites established in 2005 (two in secondary forests and two in mature forests; Chazdon et al., 2010). The secondary forest sites were used as cattle pastures after initial deforestation and varied in successional age (i.e. time since the abandonment of pasturing), 24, 24, 34, and 42 years old in 2019 and are labelled here as ES1, ES2, MS1, MS2, respectively. Three sites (MS1, MS2, MT2) are located inside La Selva, a protected landscape, while the other three are within ~6 km west of La

Selva in private properties in Chilamate, unprotected (ES1, ES2 MT1) (Table S1; Figure S1). ES and MS refer to early and mid-successional forests, and MT to mature forests. Tree and sapling inventories have been collected regularly at these sites (e.g. Dupuy & Chazdon, 2008; Guariguata et al., 1997; Norden et al., 2017). The study's experimental set-up was limited to available secondary forests within a short spatial range, resulting in a non-fully factorial design. While this allowed for comparability between secondary forests with protected and unprotected landscape conditions, the lack of an ES and MS in each protected and unprotected category should be noted.

2.2 | Seedling monitoring

Forty plot pairs (1 m²) were established in each of six forest sites (480 plots total) to census young (stems <20 cm tall), free-standing woody stems. The plot pairs were randomly distributed with a minimum distance of 2 m between each pair. Each pair consisted of two contiguous plots: a control plot lacking the enclosure and a plot surrounded on all vertical sides by the enclosure (open at the top). Exclosures were 100 cm tall, made from metal wire hardware cloth (mesh size of 1.5 cm), and reinforced with 8 mm diameter rebar at the corners. Exclosures were selectively permeable; a 20-cm square hole at the bottom edge of each exclosure allowed entry of smaller terrestrial mammals such as spiny rats but excluded LTH-mammals such as peccaries, tapirs and deer (as Kuprewicz, 2013; Figure S2). However, the study design did not distinguish among particular species of LTH-mammals.

Due to their contiguity, plots in a pair will likely experience similar seed rain (Koenig, 1999). In each plot, all free-standing woody stems <20 cm in height were tagged, identified to species and monitored every 60 days from June 2017 to September 2019. Each census recorded the seedling status as survived or dead and as recruited if it was new. All the stems newly appearing during the 2017–2019 time frame when the exclosures were deployed are hereafter referred to as 'recruited seedlings', whereas the seedlings present before the beginning of the experiment are 'established seedlings' (recorded at the first census). All seedlings once recorded in the census were followed even after they grew to more than 20 cm. Seed trait classification was sourced from previous studies in the area (Huancá-Núñez et al., 2021; Wendt et al., 2022). Specifically, seed size data were available for 73% of 116 species present and shade tolerance for 84%.

2.3 | Statistical analysis

All analyses were performed in the R statistical software (R Development Core Team, 2022). Census date is the amount of time since the enclosure treatment was imposed.

We quantified the effects of excluding LTH-mammals on the survival of seedlings in secondary and mature forests in protected and unprotected landscapes using data on 116 species censused for 26 months every 2 months (Table S2) and Bayesian survival models. We used weakly informative priors of Normal (0, 1) for variance

parameters and Student (5, 0, 2.5) for coefficients, which is considered a conservative method (Gelman et al., 2008).

Using the *brms* package in R (Bürkner, 2017) and a Weibull error distribution, we fitted right-censored survival models, analysing the time-to-event, where the disappearance of the individual seedling at the time of the census was interpreted as seedling death. First, we fitted models that included (1) enclosure treatment (categorical: enclosure versus non-enclosure), (2) forest successional stage (categorical as Mature: MT1, MT2, and Secondary: ES1, ES2, MS1, MS2) and (3) landscape protection (categorical: protected and unprotected) as fixed terms and their interactions. We included as random terms; (1) plot pair nested within site to account for the nested design; (2) species identity to allow for differences in baseline survival rates across species; (3) species-specific responses to treatment, since interspecific responses are biologically expected; (4) seedling height, to account for the effects of size on survival; and (5) tag, to account for the individual seedling effect. Comparing alternative models was done with Bayesian leave-one-out cross-validation and Watanabe Akaike Information Criterion (WAIC; Vehtari et al., 2017). Markov Chain Monte Carlo (MCMC) sampling was performed on four chains, each with 20,000 iterations, discarding the first 10,000 iterations of each chain as burn-in. Convergence was judged visually when the MCMC chains were well mixed and when $R\text{-hat}$ was ≤ 1.0 .

We used the hazard ratio (HR) to compare the effects of the enclosure treatment on seedling survival probability between enclosures and non-enclosures at the landscape and forest stage levels. An $HR > 1$ indicates higher survival in enclosures than in non-enclosures. $HR < 1$ indicates higher survival in non-enclosures than enclosures, and $HR = 1$ indicates no effect. We determined the significance of predictors when 95% credible intervals of parameter estimate excluded one.

To evaluate whether changes in survival between enclosures and non-enclosures varied with species traits, we extracted hazard ratios (HR) of the effect of enclosure treatment by species from our survival model. We then regressed species' effect size with seed size and shade tolerance in independent models as both traits are correlated ($r = 0.52$, $p < 0.01$, Figure S3). Note that the survival model fitted 116 species with 26 months of data for the community-level analysis; however, we only extracted the species HR for the 60 species with at least 10 occurrences, as species-level results are less informative for species with sparse data.

We employed four methods to assess changes in community structure defined as seedling density, diversity, and composition using 116 species (Methods S1 and Table S10). First, to assess the effect of enclosure treatment on seedling density at the plot level, we incorporated the following fixed terms and their interactions: (1) enclosure treatment, (2) census date (6, 12, 18, and 26 months) and (3) site (ES1, ES2, M1, MS2, MT1, MT2) with (1) plot nested within site as a random term. We used generalized mixed models with a Poisson error distribution. Secondly, we evaluated LTH-mammals' effect on species diversity using rarefied species richness and evenness (inverse Simpson). We calculated rarefied

species richness and evenness for each plot by site with the package INEXT (Hsieh et al., 2016). We included the same fixed and random terms as in the previous model. We determined the most-supported model using AIC model selection, and interaction terms were excluded if they did not decrease AIC by at least two units relative to a simpler model (Burnham & Anderson, 2002). We corrected for multiple t-tests across the fixed effect terms of the most-supported models using Tukey. Note that in the first and second models, to avoid complex interpretations of four-way interactions, we represented both the forest successional stage and landscape protection using the term 'site' in a viable three-way interaction, with sites ordered based on their successional age. Third, we calculated the total change in diversity (inverse Simpson) for life form (shade tolerance and seed size) from the initial (established seedlings) and final census (recruited seedlings) dates. Then, we employed a generalized linear regression with diversity as a variable response, (1) enclosure treatment, (2) census date, (3) shade tolerance as fixed terms and (1) plot within site as the random term. Fourth, to test total change in community composition, we calculated abundance-based similarity between seedling communities in enclosures and non-enclosures within each site. We compared these similarities using a paired t-test at the initial and final census dates. We estimated similarities using a bootstrap approach of 999 simulations and a Hill number of $q = 1$, using the *SimilarityMult* function, which considers both the presence and abundance of species (Gotelli & Chao, 2013) and to visualize these differences between site \times enclosure treatment combination we used NMDS as implemented by the function *metaMDS* with the Chao-Jaccard dissimilarity estimator and two dimensions evaluated by a permutational multivariate analysis of variance, as implemented in the VEGAN package.

3 | RESULTS

3.1 | Effects of mammal exclusion and landscape protection on seedling survival

The most supported survival model included the interactions between landscape protection, enclosure treatment and forest successional stage (Table S3). Survival differences were significantly higher in enclosures than non-enclosures in the protected landscape, La Selva, than in the unprotected landscape for both mature and secondary forests (Figure 1a). Nevertheless, at 26 months, the end of our experiment, the HR for seedling survival was 1.58 (CI: 1.41–1.73) and 1.43 (CI: 1.34–1.57) for the protected mature and secondary forests, respectively, indicating a 58% and 43% higher risk of seedling death outside the enclosure than inside them. In the unprotected secondary forests, the HR was 1.19 (CI: 1.11–1.31), indicating a 19% risk of seedling death outside the enclosure. However, even after 26 months, enclosure treatment did not affect seedling survival in the MT1 unprotected mature forest.

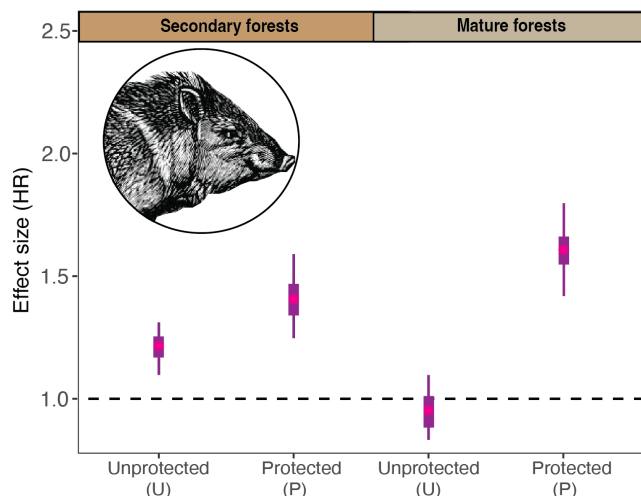


FIGURE 1 Variation in the effects of the mammal exclusion on the survival of seedlings in Costa Rican wet forests. Hazard ratio (HR) shows the effect size of mammal exclusion on (a) landscapes protected (La Selva) and unprotected (Chilamate) at mature and secondary forests on seedling survival after 26 months since the establishment of the exclosures. The central dot indicates the posterior mean HR, and the thicker line indicates 95% CI. When the 95% CI line overlaps with one, the HR indicates no effect of the LTH-mammals' exclusion on seedling survival.

3.2 | Dependence of the effects of mammals on species' traits

The effects of mammal exclusion on seedling survival varied across species (Figure 2). The positive effect of mammal exclusion on seedling survival increased as seed length increased (Figure 2a, $R^2 = 0.20$, $F_{(1,58)} = 22.44$, $p < 0.04$), and the effect was marginally more positive for shade-tolerant compared with light-demanding species (Figure 2b, $t = 1.42$, $p = 0.06$).

3.3 | Interactive effects of mammal exclusion and successional stage on the community structure of seedlings

The effect of mammal exclosures on seedling density and species diversity depended on the successional stage of the forest and the census date (Figure 3). For density and diversity, the best-supported model included the three-way interaction between treatment, site, and census date (Tables S4 and S6). In the early-successional sites (ES1, ES2) and the mature forest inside La Selva (MT2), the seedling density inside exclosures increased, ultimately becoming significantly higher than non-exclosures (Figure 3a, Table S5). For the mid-successional sites (MS1, MS2) and the mature forest outside La Selva (MT1), seedling density was not significantly affected by mammal exclusion (Figure 3a, Table S5). In the early-successional sites (ES1, ES2, MS1) and the mature forest inside La Selva (MT2), after a longer duration of mammal

exclusion, species richness became significantly higher outside exclosures than inside (Figure S4). Evenness showed a significant increase in non-exclosures compared to inside exclosures in the protected mature forests MT2 as early as 18 months, while the unprotected mature forests did not exhibit such changes. Also, although mammal exclusion only marginally affected species evenness of seedlings in all secondary forests, these sites exhibited a trend of increasing species evenness in plots outside exclosures over time, indicating a gradual decline in the abundance of dominant species (Figure 3b, Table S7).

At the initial census date, species composition had a similar evenness index in both exclosure and non-exclosures for light-demanding and shade-tolerant species, with higher variation in the latter. However, at the final census, we observed that evenness was higher at non-exclosures than inside exclosures for light-demanding and shade-tolerant species, with significantly higher evenness for light-demanding species (Figure 4a, Table S8). The similarity in species composition of seedlings inside and outside the exclosures within site declined from the initial to the final census date ($t = 6.16$, $p < 0.01$; Figure 4b, Table S9). Based on visual inspection of the community ordination, the composition of the seedling communities in exclosure and non-exclosure treatments were very similar prior to mammal exclosure (Figure 4c). However, by the end of the experiment, after 26 months of mammal exclosure, the compositions had shifted substantially (Figure 4d), with the seedlings in exclosures showing reduced variation in composition compared to seedlings in non-exclosures.

4 | DISCUSSION

LTH-mammals can alter mature tropical forests' community structure through trophic and non-trophic pathways (Dirzo et al., 2014; Luskin et al., 2019; Souza et al., 2022). However, whether these interactions recover following deforestation and operate similarly during the succession of secondary tropical forests is still unclear (Chazdon, 2014; Villar & Medici, 2021; Villar et al., 2021). Here, we investigated LTH-mammals' effects on seedling establishment and community structure of mature and secondary Costa Rican wet tropical forests. Our findings corroborate earlier studies in mature tropical forests that highlight the impact of LTH-mammals on seedling communities (Beck et al., 2013; Paine & Beck, 2007; Paine et al., 2016; Terborgh & Wright, 1994; Theimer et al., 2011). Moreover, we found that LTH-mammals impact seedling communities in successional forests even in those younger than 26 years old. Through our 26-month study, LTH-mammals not only reduced seedling survival but also led to increases in diversity and shifts in species composition. The strength of LTH-mammal exclosure effects on seedling survival was species-dependent, with pronounced positive impacts on larger-seeded species. Our study offers new insights into plant-mammal interactions in tropical forests, revealing LTH-mammals' ability to shape early forest regeneration following pasture abandonment.

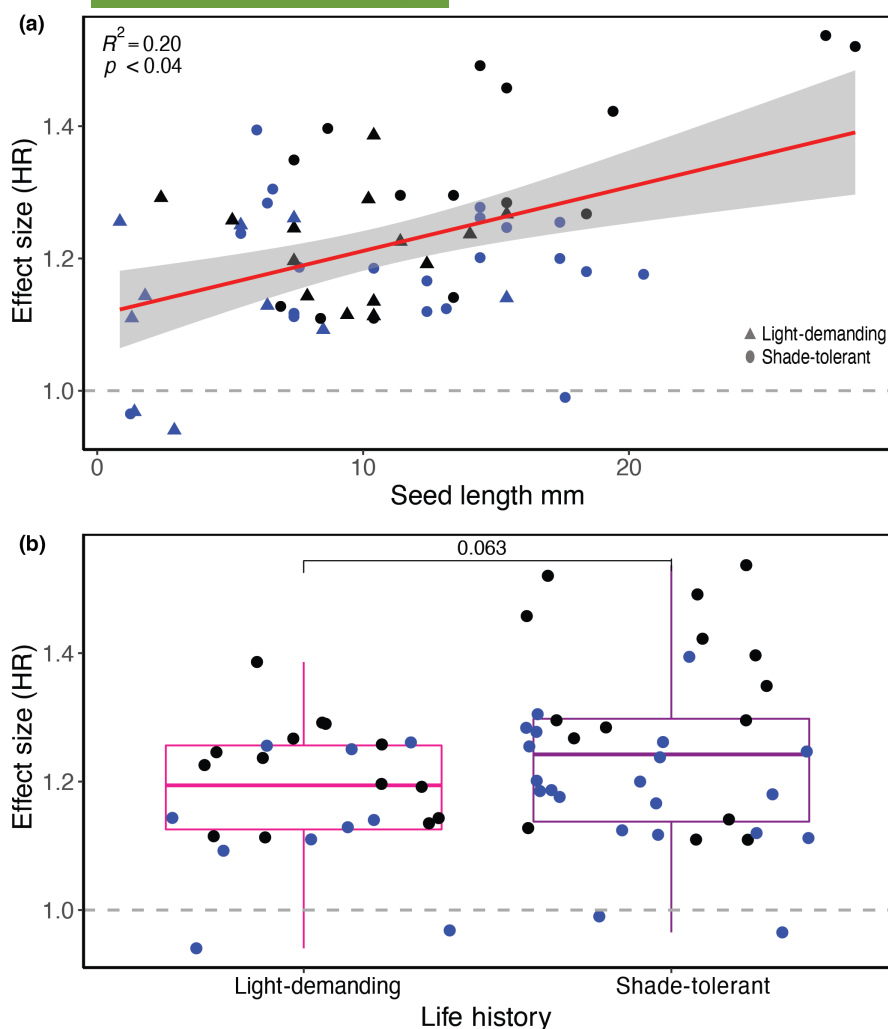


FIGURE 2 Effect of the LTH-mammals exclusion on survival of woody seedlings with 60 species' traits (seed size and shade tolerance). The hazard ratio for each species for the survival difference between exclosures and non-exclosures for (a) seed length and (b) shade tolerance. The fitted regression line and confidence band (shaded area) were generated over the posterior means. Each dot represents a parameter estimate for a species, with black symbols indicate effect sizes that are significantly different from the null hypothesis ($HR = 1$), while blue symbols indicate no significant difference. Effect size < 1 indicates survival was higher in non-exclosures than exclosures, whereas effect size > 1 indicates survival was higher in exclosures than non-exclosures.

4.1 | Effects of landscape protection and mammal exclusion on seedling survival and density

We found that the protection of forests at the landscape level and forests' successional stage explained the effect of LTH-mammals exclusion. Sites inside La Selva have been protected for ~60 years. While the scope of our study precluded the collection of data on LTH-mammals identity and abundance, studies indicate that this protection has caused LTH-mammals such as *Pecari tajacu* to become fairly abundant inside, compared to outside, La Selva (Romero et al., 2013; TEAM Network, 2020). After 26 months, we found that excluding LTH-mammals in protected sites had a greater positive effect on seedling survival than in unprotected sites. This effect was more evident in mature forests as the unprotected mature forest MT1 did not experience an effect on seedling survival from LTH-mammals exclusion, but the protected MT2 did. These results confirm prior studies showing higher seedling survival in unprotected forests than those protected from anthropogenic disturbances (Beck, 2006; Dirzo & Miranda, 1990; Terborgh et al., 2008). Moreover, the protected mature forests had significantly higher seedling density inside exclosures and evenness in non-exclosures compared to non-significant differences between exclosures and non-exclosures in the unprotected mature forest.

Our findings suggest that LTH-mammals can significantly affect seedling dynamics in young, unprotected, and protected secondary forests. This pattern may be partially explained by distance, as unprotected secondary sites were located in close proximity to the protected landscape in La Selva, making them more likely to be inhabited by LTH-mammals such as *Pecari tajacu*, which are highly abundant in La Selva. Although our study did not directly assess the effects of distance and connectivity, our results suggest that proximity to protected forests may facilitate LTH-mammals' recolonization of secondary forests (Arévalo-Sandi et al., 2018). One limitation of our study is that while we examined landscape protection and exclosure treatment effects on mature and secondary forests, we did not differentiate within ES and MS secondary forests; clearer insights would come from evaluating landscape protection and treatments within specific secondary forest categories.

Similar to previous research by Forbes et al. (2019) and Beck et al. (2013), which stressed the importance of considering exclusion duration, our study found that overall, the effects of LTH-mammals exclusion on density grew stronger with a longer duration of exclusion in mature and secondary forests. However, the temporal effects varied by site, suggesting that the experiment's duration may affect whether or not a significant exclusion effect is found. The effects of

FIGURE 3 Variation in the density and diversity of woody seedlings with forests successional age and enclosure treatment in Costa Rican wet forests. Seedling density (a) and evenness (b) in enclosures and non-enclosures at four secondary and two mature forest sites at census dates (6, 12, 18, and 26 months) with 95% confidence intervals.

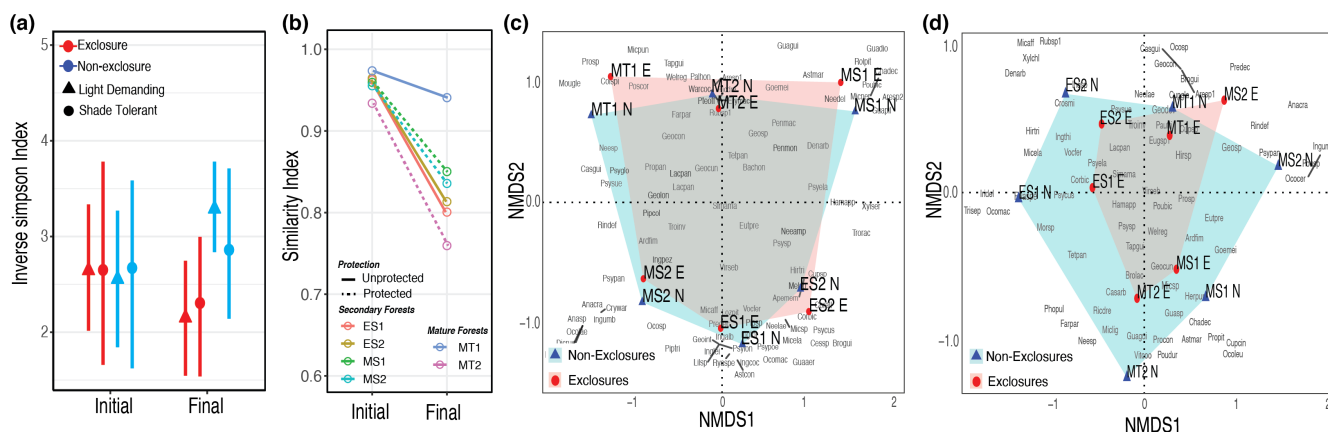
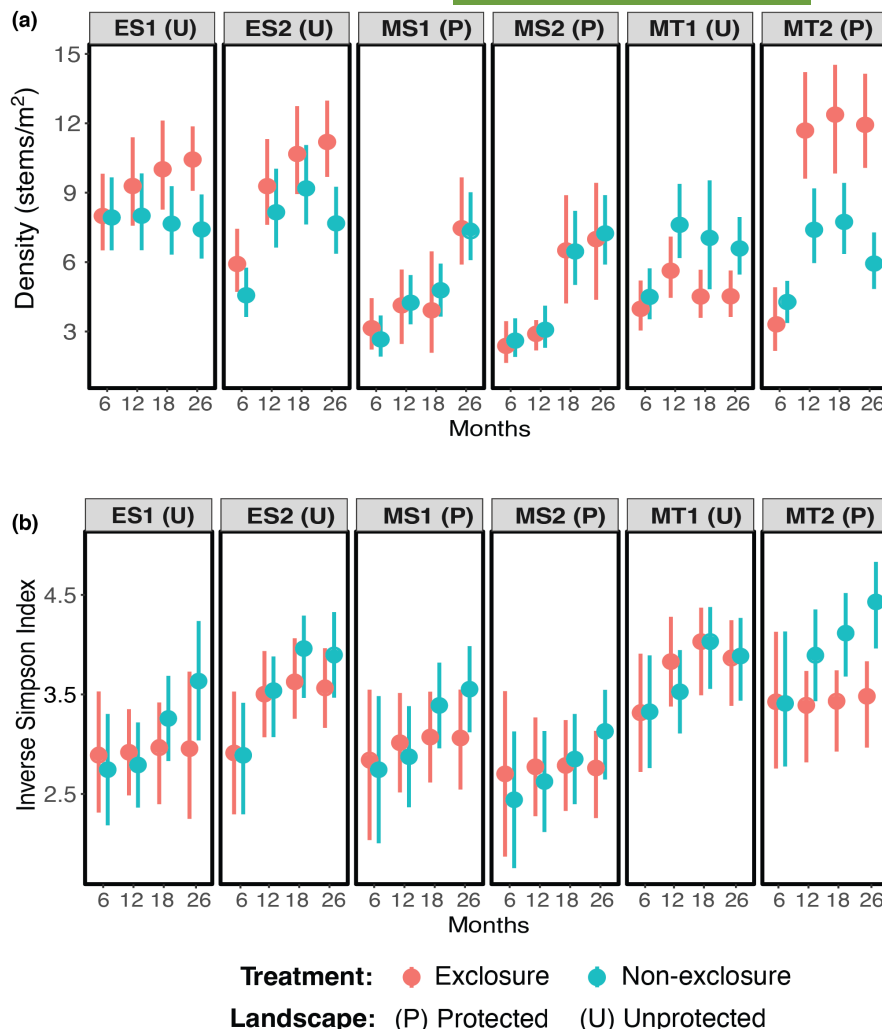


FIGURE 4 Variation in species composition of seedling communities with enclosure treatment over two census dates in Costa Rican wet forests. (a) Change in evenness by shade tolerance from the initial census and the last census date (b) Variation in similarity (Abundance-based index $q=1$) in species composition between seedlings at the initial and final census date (see Table S9); species composition of seedlings in enclosures (E) non-enclosures (N) (c) established seedlings prior to imposition of the enclosure treatment and (d) of seedlings after 26 months of enclosure treatment. Sites MS1, MS2, and MT2 are in protected landscapes. Species abbreviations are the first three letters of their genus and species name. Sites: early-successional as ES, mid-successional sites as MS, and mature sites as MT. A single ordination was performed using non-metric multidimensional scaling, in which distances in the biplot are metric, representing differences in composition and thus are on the same scale in (c) and (d). Note that Figure 4a included 93 species with available shade tolerance classification, while 4b–4d included all species.

mammal exclusion on seedling density were significant as early as 12 months in the protected mature forest but only at 26 months in two of our secondary forests. In contrast to our findings, DeMattia et al. (2006), in a 12-month-long study at Sirena Biological Station, Costa Rica, reported that terrestrial mammal exclusion did not affect seedling density in mature or secondary forests. However, in addition to the much shorter duration, their study only included *Inga marginata* and *Pterocarpus violaceus* species.

In the protected mature forest and all secondary forests, seedling diversity showed an increasing trend over time in non-exlosures corresponding to sites where LTH-mammals affected seedling density. Several studies within mature tropical forests have shown that high seedling density, particularly among conspecifics, reduces seedling recruitment (Augsburger & Kitajima, 1992; Harms et al., 2000; Russo & Augspurger, 2004). We observed that early-successional (ES) and the mature MT2 sites had higher seedling density and stronger effects of LTH-mammals, as compared to mid-successional sites (MS), indicating that the variation in the strength of LTH-mammal exclusion could be linked to variation in overall seedling density. This finding aligns with the foraging behaviour of mammalian seed and seedling predators targeting areas higher in resource availability (Galetti et al., 2015; Pyke et al., 1977). Overall, our results agree with Villar & Medici, 2021, indicating that LTH-mammals have a pronounced impact on the mature than in secondary forests. However, we argue that LTH-mammals' effects could be more closely tied to overall site seedling density. While Villar & Medici, 2021 found a stronger effect of LTH-mammals corresponding to their almost double higher species richness in their mature compared to secondary forests in Brazil, we found similar seedling richness between mature and secondary forests, consistent with previous studies in the same sites (Norden et al., 2009). Our sites, where LTH-mammals' effects were more pronounced, had significantly higher site seedling density but only slightly higher mean richness than sites with no LTH-mammals' effects. MT1, which had no effect of LTH-mammal exclusion, had a high richness similar to the control MT2 but lower site density than other sites where LTH-mammals did not have an effect. Therefore, our research suggests that the impact of LTH-mammals might be influenced by seedling site density, regardless of the successional stage.

4.2 | Effects of mammals on community structure of seedlings

Similarity in species composition of seedlings in exclosures and non-exlosures declined over 26 months from the initial to the final census date for all sites. We found a significant increase in the evenness of light-demanding species from the initial to the final census date. One explanation for this change is that exclusion differentially affected seedling survival across woody species. Supporting this, we found stronger positive effects of exclusion on the survival of larger-seeded species. One example is *Pouteria durlandii*, a shade-tolerant species with the strongest positive effect of mammal exclusion; this species' fleshy fruits and large seeds likely lure LTH-mammals, which

might damage seedlings by consuming them or trampling them in pursuit of these seeds (Hammond, 1995).

These stronger effects of LTH-mammals exclusion on larger-seeded species align with observations showing large mammals' foraging preferences for larger seeds (Forget & Jansen, 2007; Jansen et al., 2004; Martínez-Ramos et al., 2016). Similar effects were also seen in mature, wet Costa Rican forests by Kuprewicz (2013), who found that larger-seeded species experienced predation by collared peccaries (e.g., *Iriarte deltoidea*). In contrast, a study in Amazonian Peru (Paine & Beck, 2007) found that excluding large terrestrial herbivores did not affect seedling recruitment. In Amazonian sites in Brazil, white-lipped peccaries, which have a different home range and group size from collared peccaries (Akkawi et al., 2020; Bodmer, 1990) increased seedling density, but tapirs did not (Villar et al., 2021, 2022), despite being a relict megafauna species known to consume a remarkable number of seed species (355) in tropical forests (Bueno et al., 2013; Fragoso et al., 2003). Differences between the Costa Rican and Amazonian sites, including more species of terrestrial herbivores, likely owing to the largely intact populations of top predators in the Amazonian site (Rocha-Mendes et al., 2010; TEAM Network, 2020; Voss & Emmons, 1996) as well as potential differences in plant community characteristics (e.g. seed phenology), may have contributed to these contrasting findings. Therefore, future studies should not only focus on the diversity of LTH-mammals, which is crucial for maintaining tropical forest ecological function (Villar et al., 2020), but also differentiate the effects of mammals' specific species, guild, group sizes, and small-scale movement, which can be important in understanding the role of biotic factors in forest regeneration across tropical forests in different parts of the globe.

Moreover, future studies should also consider whether LTH-mammals' presence is more seasonal or permanent to understand the extent of LTH-mammals' impact on forest regeneration. For example, manipulating LTH-mammals population abundance (e.g. Koerner et al., 2018). For instance, if LTH-mammals negatively affect large-seeded species in a permanent state, their presence may significantly impact the pace and trajectory of succession, even halting forest regeneration. However, if their presence is more seasonal or spatially scattered, they may positively influence regeneration by increasing seedling diversity and preventing the invasion or dominance of any single species, including large-seeded and shade-tolerant species. Particularly, if shade-tolerant larger seed species manage to find spatial refuges, LTH-mammals will be responsible for structuring tropical forests spatially (Villar et al., 2021). Longer term studies are needed to enhance our understanding of the impact of LTH-mammals on forest regeneration, particularly in the context of climate change and the worldwide loss of LTH-mammal diversity and populations.

5 | CONCLUSIONS

The role of LTH-mammals in the regeneration and restoration of tropical forests is important to consider, especially in the context

of ongoing efforts for rewilding and ecosystem restoration during the UN Decade of Ecosystem Restoration (United Nations, 2019). Tropical forest succession involves a transition in woody species composition from smaller-seeded, faster-growing, light-demanding species to larger-seeded, slower-growing, shade-tolerant species (Boukili & Chazdon, 2017; Guariguata & Ostertag, 2001; Wendt et al., 2022). Our study suggests that in Costa Rican wet forests, LTH-mammals may affect the pace and trajectory of this transition through differential, trait-dependent effects on woody species survival. So, efforts to rewild LTH-mammals in secondary forests are important because rewilding can increase woody species diversity during succession. However, we also warn that an overabundance of these LTH-mammals could also negatively impact the pace of succession due to their preference for large-seeded plant species. Therefore, it is crucial to have a comprehensive wildlife management plan: While reintroducing LTH-mammals is needed where they have reached low population density, there must also be mechanisms for controlling their populations after rewilding, such as reintroducing large carnivores. Overall, our manipulative field experiment demonstrates that excluding LTH-mammals strongly influences the density, diversity and composition of seedling communities in mature and even young secondary tropical forests. We also suggest that LTH-mammals may be key factors contributing to the increasing compositional dissimilarity of regenerating secondary forest patches across human-modified landscapes (Huanca-Núñez et al., 2021; San-José et al., 2019).

AUTHOR CONTRIBUTIONS

Nohemi Huanca-Núñez, Robin L. Chazdon and Sabrina E. Russo conceptualized the project. NHN oversaw field data collection and conducted the data analysis. Nohemi Huanca-Núñez led the writing of the manuscript in close collaboration with Sabrina E. Russo and Robin L. Chazdon. All authors contributed to the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

No conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.8gtht76vr> (Huanca-Núñez et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Stand characteristics of six 1-ha forest sites in successional and mature wet forests in Sarapiquí, Costa Rica.

Table S2. List of codes, scientific names for all species in this study.

Table S3. Results from the top five models selected for variation in seedling survival, comparing experimental treatment.

Table S4. Results from the Top Five Models Selected for the fixed effect model of seedling density in Costa Rican wet forests.

Table S5. Summary of post-hoc tests (adjusted for multiple comparisons using Tukey's HSD) for differences in the density of seedlings inside versus outside of the exclosures across census time points (6, 12, 18, 26 months) and forest sites.

Table S6. Results from the top five models selected for the fixed factors in the diversity models.

Table S7. Summary of post-hoc tests (adjusted for multiple comparisons using Tukey's HSD) for differences in the evenness as inverse Simpson indexes inside versus outside of the exclosures across census time points (6, 12, 18, 26 months) and forest sites.

Table S8. Evenness comparisons between exclosure and non-exclosures for light-demanding and shade-tolerant species at the initial and final census.

Table S9. Abundance-based similarity ($q=1$ index) between exclosure treatment pair (protected versus unprotected) within site at the initial and final census date.

Table S10. Model approach summary.

Figure S1. Map of the study region in Sarapiquí, Costa Rica, showing the locations of the six forest plots of different successional ages.

Figure S2. Schematic experimental design for comparing survival and composition of seedlings in plots with and without exclosures.

Figure S3. Seed size (continuous variable) and shade tolerance (categorical value) Pearson—point bi-serial correlation.

Figure S4. Seedling rarefied species richness inside and outside of exclosures at four secondary and two mature forest sites at 26 months.

Figure S5. Variation in species composition of seedling communities with exclosure treatment over two census dates in Costa Rican wet forests, using 84 woody species.

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