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Predicting how defaunation-induced changes in seed predation and dispersal will affect tropical tree populations

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Article Impact Statement: Reduced seed dispersal and altered seed predation caused by defaunation may have negligible near-term effects on tropical tree populations.

Abstract

The loss of large animals due to overhunting and habitat loss potentially affects tropical tree populations and carbon cycling. Trees reliant on large-bodied seed dispersers are thought to be particularly negatively affected by defaunation. But besides seed dispersal, defaunation can also increase or decrease seed predation. It remains unclear how these different defaunation effects on early life stages ultimately affect tree population dynamics. We reviewed the literature on how tropical animal loss affects different plant life stages, and we conducted a meta-analysis of how defaunation affects seed predation. We used this information to parameterize models that altered matrix projection models from a suite of tree species to simulate defaunation-caused changes in seed dispersal and predation. We assessed how applying these defaunation effects affected population growth rates. On average, population-level effects of defaunation were negligible, suggesting that defaunation may not cause the massive reductions in forest carbon storage that have been predicted. In contrast to previous hypotheses, we did not detect an effect of seed size on changes in seed predation rates. The change in seed predation did not differ significantly between exclosure experiments and observational studies, although the results of observational studies were far more variable. Although defaunation surely affects certain tree taxa, species that benefit or are harmed by it and net changes in forest carbon storage cannot currently be predicted based on available data. Further research on how factors such as seed predation vary across tree species and defaunation scenarios is necessary for understanding cascading changes in species composition and diversity.

KEYWORDS
fragmentation, overhunting, plant–animal interactions, tree demography

Predicciones de cómo los cambios inducidos en la dispersión y depredación de semillas por la pérdida de fauna afectará a las poblaciones de árboles tropicales

Resumen: La pérdida de animales grandes debido a la caza excesiva y la pérdida del hábitat afecta potencialmente a las poblaciones de árboles tropicales y al ciclo del carbono. Se considera que los árboles que dependen de dispersores de semillas de talla grande son los más afectados negativamente por la pérdida de fauna. La defaunación también puede incrementar o disminuir la depredación de semillas, además de su dispersión. Todavía no está claro cómo afectan al final a las dinámicas poblaciones de los árboles los diferentes efectos de la pérdida de fauna en las etapas temprana de vida. Revisamos la literatura sobre cómo la pérdida de animales tropicales afecta las diferentes etapas de vida de las plantas y realizamos un metaanálisis sobre cómo la pérdida de fauna afecta a la depredación de semillas. Usamos esta información para definir los parámetros de los modelos que alteraron los modelos de proyección de matriz a partir de un conjunto de especies de árboles y así simular los cambios causados por la pérdida de fauna en la dispersión y depredación de semillas. Analizamos cómo la aplicación de estos efectos de pérdida de fauna afectó las tasas de crecimiento poblacional. En promedio, los efectos de la pérdida de fauna a nivel

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poblacional fueron no significativas, lo que sugiere que la pérdida de fauna puede no ser la causa de las reducciones masivas que se han pronosticado en el almacenamiento de carbono forestal. Contrario a las hipótesis previas, no detectamos ningún efecto del tamaño de las semillas sobre los cambios en las tasas de depredación. El cambio en la depredación de semillas no difirió significativamente entre los experimentos de encierro y los estudios de observación, aunque los resultados de los últimos fueron mucho más variables. Mientras que la pérdida de fauna seguramente afecta a ciertos taxones de árboles, actualmente no se pueden pronosticar, con base en los datos disponibles, las especies que se benefician o perjudican por esta pérdida y los cambios netos en el almacenamiento de carbono forestal. Se necesita una investigación más avanzada sobre cómo varían los factores, como la depredación de semillas, entre especies de árboles y escenarios de pérdida de fauna para entender los cambios en cascada en la composición y diversidad de las especies.

PALABRAS CLAVE
demografía de árboles, fragmentación, interacciones planta-animal, caza excesiva

【摘要】
因过度捕猎和栖息地丧失引起的大型动物丧失可能会影响热带树木种群数量和碳循环。人们认为, 依赖大体型种子传播者的树木尤其会受到动物灭绝的不利影响。但除了种子传播之外, 动物灭绝还会增加或减少动物对种子的取食。目前尚不清楚不同的动物灭绝对树木早期生命阶段的影响最终将如何影响树木的种群动态。本文回顾了关于热带动物丧失影响植物不同生命阶段的文献, 并对动物灭绝如何影响种子受到的取食进行了荟萃分析。我们利用这些信息调整模型参数, 改变了一组树种的矩阵预测模型, 以模拟动物灭绝引起的种子传播及受取食的变化。我们还评估了应用这些动物灭绝效应对植物种群增长率的影响。平均而言, 动物灭绝对植物种群水平的影响可以忽略不计, 表明动物灭绝可能不会导致预测中的森林碳储量大幅下降。与已有假设相反, 我们没有发现种子大小会影响种子的受取食率。种子受取食的变化在圈地实验和观测研究之间没有显著差异, 尽管观测研究的结果变异更大。虽然动物灭绝肯定会影响到某些树木类群, 但根据现有数据, 目前还不能预测因动物灭绝而受益或受到伤害的物种及森林碳储量的净变化。为了了解物种组成和多样性的级联变化, 还需要进一步研究取食种子等因素在不同树种和动物灭绝情景下的变化。**【翻译:胡怡思;审校:聂永刚】**

关键词: 破碎化, 过度捕猎, 动植物互作, 树木种群统计

INTRODUCTION

Large vertebrates are being extirpated across the tropics due to unsustainable hunting and habitat fragmentation, which affects the myriad tree species that interact with these animals (Dirzo et al., 2014; Kurten, 2013). Such defaunation can affect plants in several ways. Deprived of large vertebrate vectors, many more seeds can be left under parent trees where, as predicted by the Janzen–Connell hypothesis, they face increased distance- or density-dependent mortality due to natural enemies (Song et al., 2021). Reduced dispersal may then cause declines in some tree populations (Brodie et al., 2009; Culot et al., 2017; Rogers et al., 2017). Because many trees dispersed by large vertebrates are themselves large or have dense wood, defaunation may even induce shifts in tree species composition that reduce the aboveground biomass of tropical forests, which has implications for the global carbon cycle (Bello et al., 2015; Brodie & Gibbs, 2009; Osuri et al., 2016; Peres et al., 2016). Hunting-induced loss of vertebrates could also lead to compensatory increases in populations of small granivores, increasing seed mortality (Galetti et al., 2015; Kurten & Carson, 2015; Rosin & Poulsen, 2016). However, many of the hunted vertebrates are potent seed predators themselves, so removing these animals could benefit regeneration in certain plant species (Donatti et al., 2009; Roldán & Simonetti, 2001), though other seed enemies, such as insects and fungi, may compensate when vertebrate predation is reduced (Peguero et al., 2017; Williams et al., 2021). Defaunation can also affect other interactions between vertebrates and plants, such as herbivory and physical damage through trampling or felling (Gardner et al., 2019; Luskin et al., 2017; Rosin et al., 2017). Though these multiple effects of defaunation are understood separately, it remains unclear how these changes ultimately and cumulatively affect tropical tree populations and communities.

Previous studies on how defaunation affects trees (particularly those examining forest carbon impacts) focused almost exclusively on reduced seed dispersal. These studies often simulated community composition in defaunated forests by removing tree species that are dispersed by large vertebrates or that have large seeds and show that this can result in substantial reductions in aboveground biomass (i.e., carbon storage). The empirical evidence on carbon dynamics in defaunated forests, however, is less clear. Populations of a tree species that significantly contributed to carbon stocks are indeed declining in defaunated forests in the Brazilian Atlantic Forest (Culot et al., 2017), but hunting-induced dispersal limitation appears to have no impact on cumulative aboveground biomass at a site in Malaysian Borneo (Harrison et al., 2013).

Though it is known that tree species reliant on large-bodied dispersers will face reduced seed dispersal, it is not known how defaunation will change seed predation. Granivory may increase (Culot et al., 2017; Galetti et al., 2015; Rosin & Poulsen, 2016) or decrease (Beckman & Muller-Landau, 2007; Roldán & Simonetti, 2001; Wright et al., 2000) for different tree species under defaunation, and seed predation by insects and fungi further complicate the picture (Lamperty et al., 2020; Peguero et al., 2017; Williams et al., 2021). Mendoza and Dirzo (2007) hypothesized that trees that produced smaller seeds, whose small-bodied predators would likely remain extant even in highly defaunated systems, would face higher predation pressure than larger-seeded tree species whose predators would be eliminated by overhunting. Therefore, under defaunation, seed predation is thought to increase for smaller-seeded species and decrease for larger-seeded species, though there is limited empirical evidence to evaluate this hypothesis (Kurten, 2013). Many studies of defaunation and seed predation have used vertebrate exclosures to simulate defaunation, but results from exclosure experiments are often very different from real defaunated forests (Gardner et al., 2019; Kurten & Carson, 2015). For example, species richness tends to decline in defaunated forests, whereas species richness increases in exclosures (Kurten & Carson, 2015). This striking difference has been attributed to increased seed predation in defaunated forests due to increased populations of seed predators, compared with a decrease in seed predation and herbivory in exclosures. However, the effect of real versus experimental defaunation on seed predation rates has not been compared systematically.

Given the multiple effects of defaunation and differences in life histories among tree species, it is difficult to predict how defaunation will ultimately affect forest composition and biomass. Ideally, predictive models in ecology would be realistic, precise, and generalizable, though, in practice, ecological models can only have two of these three properties (Levins, 1966). Much of the knowledge of how defaunation affects forests comes from detailed population models of individual species (e.g., Brodie et al., 2009; Rogers et al., 2017), which are realistic and precise but not generalizable across whole forests. There are also forest-wide models based on broad assumptions (e.g., Bello et al., 2015; Chanthorn et al., 2019; Osuri et al., 2016; Peres et al., 2016) that produce precise and generalizable predictions but ignore certain defaunation impacts (such as altered seed predation) and gloss over demographic differences among tree species. Although these approaches are useful, there is a need to address the knowledge gaps by building models that are realistic (based on known biological mechanisms) and generalizable (applicable to multiple species). Such models are necessarily less precise (e.g., do not allow calculation of changes in carbon storage across forests) but would provide an understanding of how the impacts of defaunation may ultimately affect population dynamics.

We synthesized data on defaunation and tropical tree demography to build mechanistic models that assess how defaunation-caused changes in seed predation and dispersal may affect tropical tree populations. We collected data on defaunation effects from meta-analyses and a literature search and applied these effects to tropical and subtropical tree matrix projection models to assess how tree population dynamics may be ultimately affected by defaunation while considering the impacts of seed predation and seed dispersal. We also assessed whether defaunation-caused changes in seed predation could be predicted by seed size, as predicted by Mendoza and Dirzo (2007), and whether changes in seed predation differ between experimental exclosure studies and observational studies of real defaunated forests.

METHODS

Defaunation effects on tree vital rates

We searched the literature to assess how defaunation affected changes in seed predation and dispersal. For seed predation, we conducted a literature search to compile the change in seed predation rate after defaunation (P). We looked through the studies used in Kurten's (2013) defaunation meta-analysis, selecting studies that included diaspores predated, seed predation, seeds destroyed, or seeds predated as the response variable. We did not include studies with seed removal as the response variable because many of these studies used seed removal as a measure of seed dispersal. We also looked through the original studies used in Gardner et al.'s (2019) defaunation meta-analysis and Jia et al.'s (2018) exclosure meta-analysis, selecting studies that measured seed predation. To supplement these meta-analyses, we searched the ISI Web of Science database with the terms *seed predation* and *defaunation* for studies published in 2012 or later (i.e., after Kurten's meta-analysis).

We selected studies that measured seed predation rates of native species in both defaunated and nondefaunated conditions. Exclosure experiments were included, where seeds in large-animal exclosures were considered defaunated. For all these studies, we extracted the defaunated and nondefaunated seed predation rates and calculated the effect size with the odds ratio for change in seed predation (P, the ratio of the defaunated rate divided by nondefaunated rate). We removed instances where seed predation in the baseline scenario was 0% because this would cause there to be a zero in the denominator when we calculated P. Where results were presented graphically, we extracted values with WebPlotDigitizer (Rohatgi, 2019). In total, we found 73 paired defaunated and nondefaunated seed predation values in 27 studies (Appendix S2).

For seed dispersal, we compiled the proportion of seeds dispersed before and after defaunation (d and d', respectively), taken from Kurten's (2013) meta-analysis, to calculate the odds

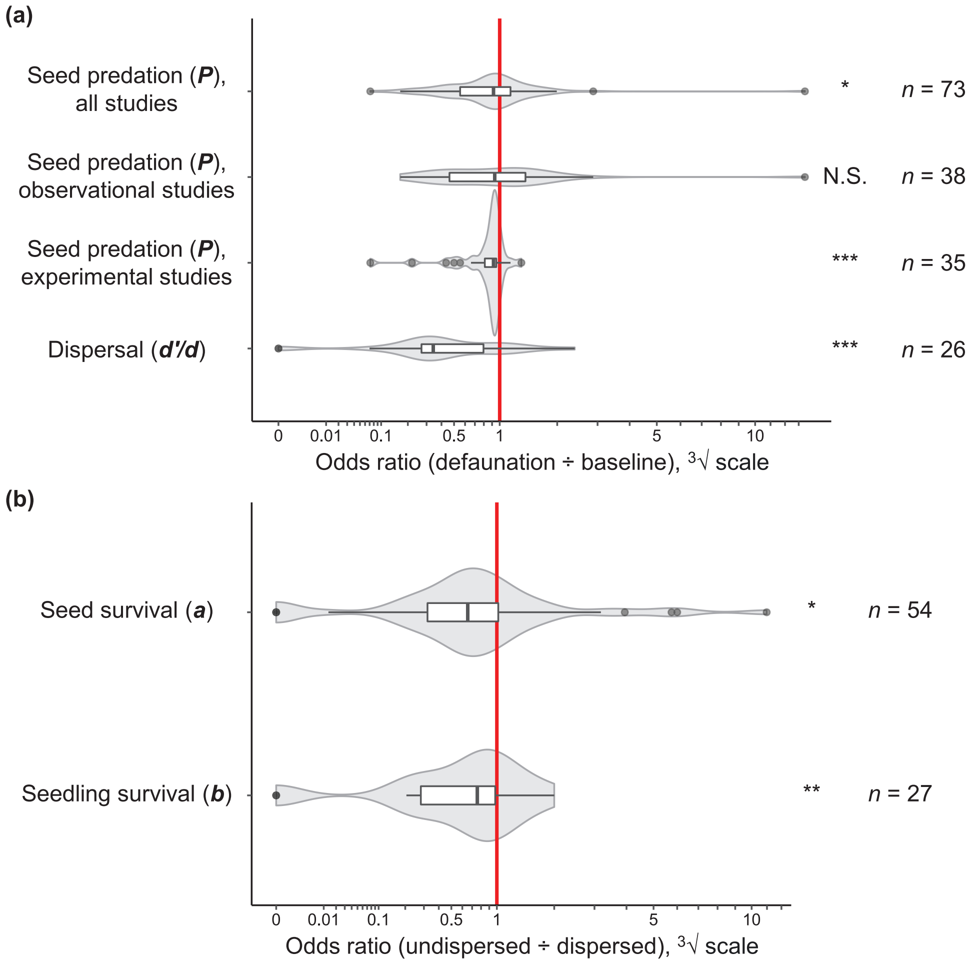

FIGURE 1 Distributions of (a) defaunation-related changes in seed predation and dispersal in a meta-analysis of defaunation effects and (b) differences in survival between undispersed and dispersed seeds and seedlings, which were used to parametrize models (1, no change between defaunation and baseline rates or between undispersed and dispersed survival; N.S. $p \geq 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ [one-sample Wilcoxon signed rank tests]). All values and the references for the original studies from which these values were calculated are in Appendices S2–S5. Seed predation data in (a) from our own meta-analysis; dispersal data in (a) from Kurten (2013); all data in (b) from Song et al. (2021). Cube-root scales are shown rather than log scales because the datasets contain zeroes that could not be log-transformed

ratio (Appendix S3). We also compiled the odds ratios for the difference in survival between dispersed and undispersed seeds (a) and the difference in survival between dispersed and undispersed seedlings (b); we used values from Song et al.'s (2021) meta-analysis (Appendices S4 & S5). All these values are from field studies of tropical tree species that compared survival rates between seeds or seedlings placed in high-density treatments or near parent trees (i.e., undispersed) versus those placed in low-density treatments or far from the parent trees (i.e., dispersed). For a and b, we used only values from species that are biotically dispersed. In the few cases where multiple dispersed versus undispersed seed or seedling comparisons were listed for a single species in a single study, we calculated the average undispersed survival and average dispersed survival. The full lists of values for P, d, d', a, and b and references for the original studies from which these values were calculated are in Appendices S2–S5, and the values are in Figure 1.

To test whether our parameters significantly differed from 1, we ran 1-sample Wilcoxon signed rank tests in R 3.5.1 (R Core Team, 2018). We tested whether defaunation significantly affected seed predation ($P \neq 1$), whether defaunation significantly affected dispersal probability ($d'/d \neq 1$), whether survival differed between undispersed and dispersed seeds ($a \neq 1$), and whether survival differed between undispersed and dispersed seedlings ($b \neq 1$).

To test whether P was affected by seed mass, as predicted by Mendoza and Dirzo (2007), we compiled seed mass data for all the species for which we had values of P (Appendix S2). When available, we extracted seed mass data from the same studies that reported change in seed predation. Otherwise, we used seed mass data from the TRY database (Kattge et al., 2011). We ran a linear regression in R 3.5.1 (R Core Team, 2018) to test whether the change in seed predation (log odds ratio) was predicted by log seed mass, study design, or the interaction between log seed mass and study design. *Study design* refers to whether the study compared separate defaunated and nondefaunated sites (observational) or whether the study used exclosure experiments at a single site (experimental).

Tropical tree population models

To assess how defaunation-induced changes in seed dispersal and predation rates might affect tree populations, we first obtained tropical tree population matrix projection models from the COMPADRE Plant Matrix Database (Salguero-Gómez et al., 2015). Matrix projection models are a type of structured population model in which vital rates, such as growth, survival, and fecundity, are used to model equilibrium population dynamics (Salguero-Gómez et al., 2015). These models divide a population into distinct stages (e.g., seed, seedling, etc.) and use vital rates collected in the field to quantify the probabilities of transitioning between stages or remaining in the same stage. The matrix constructed from these probabilities can be used to model population dynamics. We obtained population matrices for 47 tropical tree species in 19 families (Appendix S6). Population matrices were included in the analysis if they were classified as tree or palm; were from tropical or subtropical regions; did not include clonal reproduction; included life stages that could be categorized as a seedling, juvenile, and adult stage classes; included transitions between major stages; included populations in unmanipulated or unmanaged habitat treatments (i.e., not harvested or experimentally manipulated); were native species; and were from study sites that were not already defaunated. We determined whether study sites were defaunated by searching the literature. Whether a site is defaunated or not is not a clear dichotomy, and all forests vary in the proportion and types of species that have been lost. We provide the evidence we used to determine the defaunation status in Appendix S7. For most species (60%), we were able to determine from the literature that the study sites were not defaunated. However, for the remaining species, we could not assess the status of fauna at the study site. We compared analyses that included only known nondefaunated sites and analyses that included both nondefaunated sites and sites where we could not determine the defaunation status of the site, and we found no qualitative differences in the results (Appendix S8). Therefore, we report here the results from analyses that included nondefaunated sites and sites with unclear defaunation status to increase the sample size.

For species with multiple population studies that fit these criteria, we selected the study that included the most populations. For studies with more than one demographic transition matrix for a given species (53% of species), we averaged matrix elements across populations to create a composite matrix representative of that species. We also conducted a separate analysis in which we randomly selected a single matrix to represent each species; this sensitivity analysis showed that averaging matrix elements across populations did not affect the inference of our study (Appendix S8).

We reduced the sizes of each matrix to 4 × 4 with the following stages: seed, seedling, juvenile, and adult (Figure 2a). If a matrix had multiple subclasses in a single stage (e.g., multiple adult size classes), we combined stage classes such that the new composite matrix had the same stable stage distribution and the same asymptotic growth rate (λ) as the original matrix (Yearsley & Fletcher, 2002). We followed the definition of *seedling* used in each study (i.e., either plants with a diameter at breast height <1 cm or individuals under a certain height; exact threshold varied across species). *Juvenile* encompassed nonreproductive stages between seedling and adult. If matrices lacked a seed stage (i.e., fecundity was defined as the number of seedlings produced), we used seed survival values from the original published studies to create a seed stage. Of the 47 tree species, 13 lacked seed survival data, including six of the 21 large-vertebrate-dispersed species. For these species, we created a seed stage using the average seed survival value among cycads or noncycads. We divided our data in this way because cycads had significantly higher seed survival than other major lineages (i.e., eudicots and monocots), but seed survival did not differ significantly among these other clades (Appendix S11). Based on a sensitivity analysis, the use of averaged seed survival values did not affect the inference of our study (Appendix S8). No regression transitions, such as juveniles becoming seedlings, were allowed.

We defined tree species as large-vertebrate-dispersed if the list of their vertebrate dispersers included any mammals that are relatively large-bodied (i.e., excluding rodents in the families Muridae, Sciuridae, Heteromyidae, Cricetidae, and Echimyidae) or any birds that are relatively large-bodied (i.e., excluding noncorvid passerines). Lists of dispersers were obtained from the TRY database (Kattge et al., 2011) if possible and from the literature if not (information sources for all species is in Appendix S6). Because defaunation disproportionally affects large- and medium-bodied animal populations (Bogoni et al., 2022), defaunation should affect seed dispersal of these large-vertebrate-dispersed species, whereas defaunation should not affect seed dispersal of abiotically dispersed species or species exclusively dispersed by small vertebrates. For our analyses that only involved changes in seed dispersal, we included only large-vertebrate-dispersed species; for analyses that involved changes in seed predation, we included all species.

Modeling defaunation impacts on tree populations

To explore how defaunation could affect tree populations, we ran simulations that applied defaunation impacts to tropical tree population matrices. We ran 10 versions of our model. For each version, we used the 4 × 4 population matrix model of a given species (Figure 2a) to construct both a baseline population matrix and a defaunated population matrix. We then calculated λ (the asymptotic population growth rate) for both the baseline population matrix and the defaunated population matrix, and we calculated the difference in λ. We ran 5000 simulations

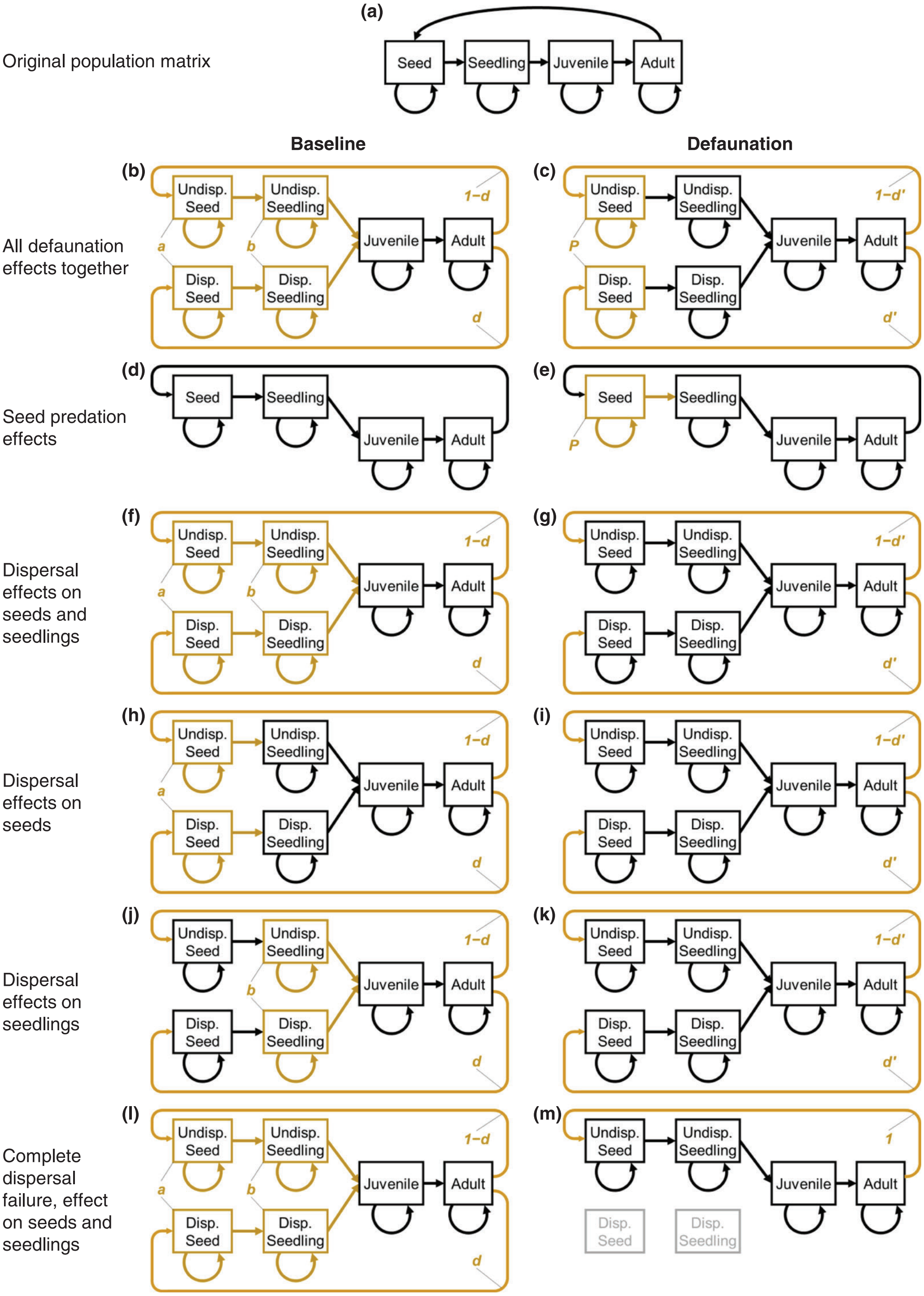

FIGURE 2 Life cycle diagrams representing different versions of the model of defaunation effects on tropical tree population dynamics: (a) COMPADRE database population matrices fit to a four-stage population matrix model used to construct a baseline (b, d, f, h, j, l) and defaunation (c, e, g, I, k, m) population matrix model for each species; (b, c) overall model with seed predation and seed dispersal effects; (d, e) seed predation models (*P*, parameter used to alter seed survival in the defaunation scenario); (f, g) dispersal model with effects on both seeds (*a*, parameter used to set the difference in survival between undispersed and dispersed seeds) and seedlings (*b*, parameter used to set the difference in survival between undispersed and dispersed seedlings); (h, i) dispersal model with effects on seeds; (j, k) dispersal model with effects on seedlings; (l, m) models of complete dispersal failure with effects on seeds, seedlings, or both. For dispersal models, (b, f, h, j, l) dispersal probability in the baseline scenario set to *d*; (c, g, i, k) dispersal probability in the defaunation scenario set to *d'*; (m) dispersal probability set to 0 in models of complete dispersal failure

of each version of the model. In each iteration, we randomly selected values for the parameters included in that version of the model (P, d and d', a, and b) from the lists in Appendices S2–S5, and calculated the difference in λ for all applicable tree species.

The 10 versions of our model were an overall model that included changes in seed predation and changes in seed dispersal that affected both seeds and seedlings (Figure 2b,c); a seed predation model that included parameter values from all seed predation studies (Figure 2d,e); a seed predation model that included parameter values from observational seed predation studies; a seed predation model that included parameter values from experimental seed predation studies; a dispersal model that included effects on both seeds and seedlings (Figure 2f,g); a dispersal model that included effects on seeds (Figure 2h,i); a dispersal model that included effects on seedlings (Figure 2j,k); a model of complete dispersal failure that included effects on both seeds and seedlings (Figure 2l,m); a model of complete dispersal failure that included effects on seeds; and a model of complete dispersal failure that included effects on seedlings.

For seed predation models, we applied parameter P to seed survival for the defaunation matrices (Figure 2e). For dispersal models that included effects on seeds, we first used parameter a to set different survival rates for undispersed and dispersed seeds (Figure 2f,h). Similarly, for dispersal models that included effects on seedlings, we used parameter b to set different survival rates for undispersed and dispersed seedlings (Figure 2f,j). For all dispersal models, we set the dispersal probability to d in the baseline matrices (Figure 2f,h,j) and then set the dispersal probability to d' for the defaunation matrices (Figure 2g,i,k). Our overall model included all these effects (Figure 2b,c). For our dispersal failure models, we first set up baseline matrices as described above for the dispersal models (Figure 2l). Then, we set the dispersal probability to zero for the defaunation matrices (Figure 2m). Detailed methods for how we applied parameters to vital rates are presented in Appendix S1.

Our seed predation models included all 47 tropical tree species. Our dispersal models and dispersal failure models included only the 21 large-vertebrate-dispersed tree species. Our overall model included all 47 tree species, but only applied changes in dispersal to the large-vertebrate-dispersed species. For other species, we kept the same dispersal probability for both baseline and defaunated matrices. We ran sensitivity analyses for the overall model and the seed predation models to compare results when including all tree species and when including only large-vertebrate-dispersed tree species. The dissimilarity between the distributions of differences in λ was negligible (Appendices S8 & S12).

Model output

With 5000 iterations drawing combinations of parameter values and 47 or 21 species included depending on the model version, each version of our model resulted in 235,000 or 105,000 values for the difference in λ. Given the arbitrary and artificially high sample size, it was inappropriate to apply frequentist statistical methods to these results. Therefore, we present the median values and interquartile range (IQR) to convey the distribution of values. We also calculated the overlapping coefficient (OVL) with the overlapping package (Pastore, 2018) version 1.7 to calculate the percent overlap between two kernel densities. Furthermore, we calculated Cliff's delta with the effsize package (Torchiano, 2020) version 0.8.1 to quantify the degree to which two distributions differed. Cliff's delta is a nonparametric measure of effect size, similar to Cohen's d; its values range from 0 to 1. We considered a value of Cliff's delta < 0.11 to indicate that the difference between groups was negligible, based on Vargha and Delaney's (2000) interpretations of their A statistic, which is related to Cliff's delta. We used OVL and Cliff's delta for sensitivity analyses (Appendix S8) and to compare results among model versions (Appendix S9). These analyses were all done in R 3.5.1 (R Core Team, 2018).

RESULTS

Through our literature review, we found that, on average, defaunation slightly decreased seed predation (one-sample Wilcoxon signed rank test, median = 0.918, 95% CI 0.794–0.979, p = 0.028) (Figure 1a). For observational studies, however, defaunation did not significantly alter seed predation (median = 0.934, 95% CI 0.760–1.198, p = 0.785), whereas experimental studies that simulated defaunation (e.g., with exclosures) significantly reduced seed predation (median = 0.918, 95% CI 0.800–0.933, $p < 0.001$). The change in seed predation was also much more variable in observational studies than in experimental studies. Based on data from Kurten (2013), defaunation significantly reduced seed dispersal; dispersal probability under defaunation was reduced by about two-thirds (median = 0.343, 95% CI 0.286–0.698, $p < 0.001$) (Figure 1a). Based on data from Song et al. (2021) and only including data from biotically dispersed species, undispersed seeds had lower survival than dispersed seeds (median = 0.654, 95% CI 0.532–0.943, p = 0.023), and undispersed seedlings had lower survival than dispersed seedlings (median = 0.757, 95% CI 0.511–0.940, p = 0.007) (Figures 1b).

Change in seed predation under defaunation was not predicted by seed mass ($p = 0.725$, $\beta = -0.033$, SE = 0.092) or by study design (observational vs. experimental, $p = 0.613$, $\beta = 0.458$, SE = 0.903). The relationship between change in seed predation and seed mass did not differ depending on whether the study was observational or experimental ($p = 0.692$, $\beta = -0.046$, SE = 0.116; multiple regression $F_{3,69} = 0.543$, multiple $R^2 = 0.023$) (Figure 3).

On average, across all combinations of defaunation effects and tree species, defaunation had very little effect on population growth rates. When all defaunation effects were applied, the median difference in λ was 0.0020 (IQR −0.0047 to 0.0198) (Figure 4), meaning that defaunation increased the population growth rate by 0.2%. The effect of seed predation differed when using parameter values from observational versus experimental studies. Using observational studies, defaunation had no effect on λ on average (median = 0.0006, IQR −0.0170

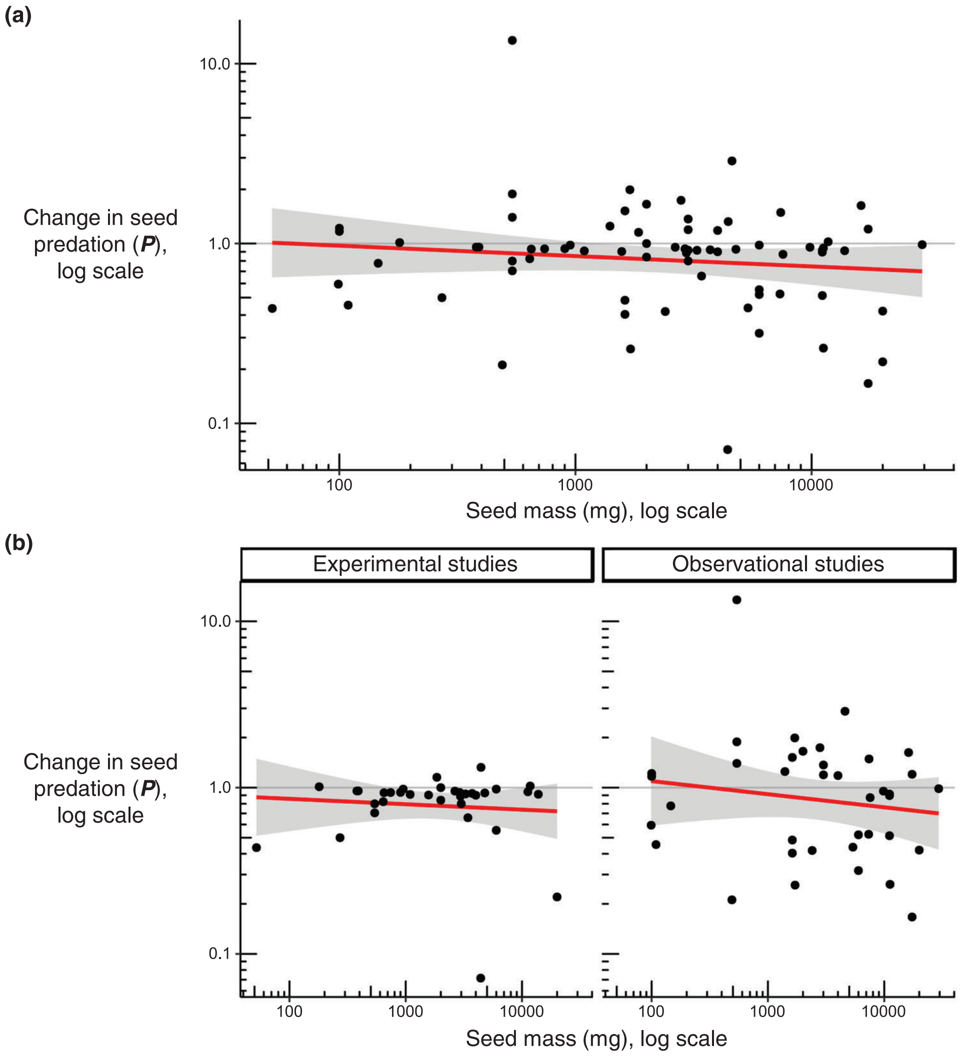

FIGURE 3 Relationship between seed predation and seed mass in studies of defaunation effects on seed predation (*P*, change in seed predation, the odds ratio for defaunated vs. baseline): (a) change in seed predation for all defaunation studies and (b) change in seed predation due to defaunation in experimental manipulations and observational studies

to 0.0231), while defaunation slightly increased λ when using experimental studies (median = 0.0041, IQR 0.0005–0.0183) (Figure 4). Seed dispersal effects alone had practically no effect on λ, whether seed and seedling effects were applied together (median = −0.0008, IQR = −0.0098 to 0.0005) or separately (seeds, median = 0, IQR −0.0026 to 0.0006; seedlings, median = −0.0005, IQR −0.0055 to 0) (Figure 4). The distributions of difference in λ differed between seed predation models and dispersal models (Cliff's delta = 0.182–0.421, OVL 31.2–42.2%) (Appendix S9).

When we simulated complete dispersal failure, the median difference in λ was −0.0043 (IQR −0.0256 to 0) (Figure 4), meaning that dispersal failure decreased the population growth rate by 0.43%. Dispersal failure reduced λ more strongly when applied to seedlings (median = −0.0026, IQR −0.0149 to 0) than when applied to seeds (median = −0.0005, IQR −0.0072 to 0.0007), though this reduction in λ was still small (Figure 4). The distributions of difference in λ differed between the three dispersal failure models and their dispersal model counterparts (Cliff's delta = 0.155–0.229, OVL 65.3–68.6%) (Appendix S9).

DISCUSSION

The loss of large vertebrates due to factors such as overhunting and habitat fragmentation can affect many plant–animal interactions; consequences range from altered dynamics of particular populations (Brodie et al., 2009; Culot et al., 2017) to hypothesized declines in forest carbon storage (Bello et al., 2015; Chanthorn et al., 2019; Peres et al., 2016). But the understanding of how the impacts of defaunation on early plant life stages ultimately affect populations across different species is still limited. Our results suggest that, on average, the defaunation effects of altered seed predation and reduced seed dispersal may have negligible influence on tropical tree populations, at least in the near term. Previous researchers assumed that

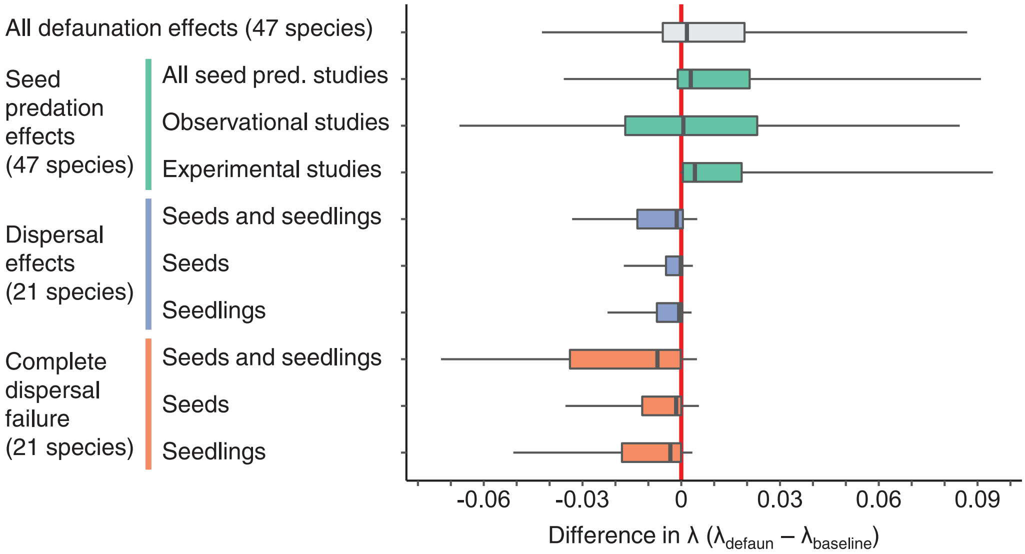

FIGURE 4 Differences in asymptotic population growth rate (λ) caused by defaunation for 10 different versions of the model of defaunation effects on tropical tree population dynamics: overall with seed predation and dispersal effects; seed predation with parameter values from all studies; seed predation with parameter values from only observational studies; seed predation model with parameter values only from experimental (exclosure) studies; seed dispersal with effects on seeds and seedlings; seed dispersal with only effects on seeds; seed dispersal with only effects on seedlings; dispersal failure with effects on seeds and seedlings; dispersal failure with only effects on seeds; and dispersal failure with only effects on seedlings (0, applying defaunation effects results in no change in λ; −0.01, defaunation decreases the population growth rate [λ] by 1%; sample sizes, number of species multiplied by 5000 iterations; boxes, interquartile ranges [25th percentile to 75th percentile]; thick vertical lines, medians; whiskers, 10th percentiles and 90th percentiles; outliers [$<$ 10th percentile or $>$ 90th percentile] not shown)

defaunation-induced losses of seed dispersal would inevitably lead to severe population declines and thus predicted that dispersal limitation could reduce carbon storage across broad swaths of the tropics (Bello et al., 2015; Brodie & Gibbs, 2009; Chanthorn et al., 2019; Dantas de Paula et al., 2018). However, given the small effects of dispersal limitation that we found, even assuming complete dispersal failure, defaunation may not necessarily cause the predicted widespread replacement of heavy-wooded, large-vertebrate-dispersed species by lighter-wooded species with other means of dispersal. Whether defaunation will result in major losses of forest carbon in the near term, therefore, remains unclear. This is consistent with empirical observations that not all defaunated forests exhibit declines in biomass (Bagchi et al., 2018; Harrison et al., 2013). The parameters we used to model the effects of seed dispersal loss were taken from experimental studies, rather than observed dispersal loss. The differences in survival between dispersed and undispersed seeds and seedlings may be quite different in real defaunated forests compared with experimental treatments. However, these experimental results are the best data available to quantify the effects of seed dispersal loss. Although seed dispersal loss may severely threaten some tree species, our results highlight that it is unjustified to broadly assume that seed dispersal loss will lead to extinction, at least in the short to medium term, even for trees thought to be dispersed by large vertebrates susceptible to overhunting.

Although the overall impact on tree populations was negligible, our results highlight the tremendous variability in how defaunation alters seed predation. In exclosure studies, seed predation rates are consistently reduced, though only slightly. In real defaunated forests, though, seed predation greatly increased in some cases and greatly decreased in others, in contrast to the consistent increase in seed predation that had been predicted (Kurten & Carson, 2015). In empirical studies, species differ widely in how seed predation rates change in response to defaunation, even within the same forest (Guariguata et al., 2000; Rosin & Poulsen, 2016). For example, in a study from Costa Rica, seed predation was higher in the defaunated than nondefaunated site for two species, lower for two others, and unchanged for two more (Guariguata et al., 2000). In contrast to Mendoza and Dirzo's (2007) hypothesis, we found that seed size did not predict predation pressure. Other traits, such as chemical compounds or seed hardness, likely play a role in how defaunation affects seed predation (Rosin & Poulsen, 2016). Different changes in seed predation may also reflect differences in the granivore communities across tropical forests. Furthermore, nonvertebrate seed enemies, such as insects and fungi, may compensate for reduced seed predation, so reduced vertebrate seed predation may not significantly affect seed survival (Peguero et al., 2017; Williams et al., 2021). To add even more complexity, some vertebrates prey upon specialist insect seed predators, so extirpating these vertebrates could release insect seed predator populations (Peguero et al., 2017). The highly variable effects of altered seed predation on population dynamics that we found indicate that some species may be severely affected, even while most species are unaffected. However, data are not currently available to predict how defaunation will change seed predation for particular species or systems.

An important aspect of defaunation that we did not examine here is the effect of defaunation via changes in herbivory, trampling, or other physical damage (Gardner et al., 2019; Rosin et al., 2017). Reductions in herbivory and trampling, rather than increases in seed predation, may explain the consistent increase in species richness observed in experimental exclosures (Kurten & Carson, 2015). Reduced trampling by large vertebrates can increase seedling survival, but so far, only a few studies have quantified how defaunation affects plant vital rates via trampling (Roldán & Simonetti, 2001; Rosin et al., 2017). Removing large-bodied ecosystem engineers, such as elephants or wild pigs, may affect older plant life stages (Luskin et al., 2017; Poulsen et al., 2018) and have significant impacts on local plant communities (Luskin et al., 2021). For example, nest building by wild boar (*Sus scrofa*) in Pasoh, Malaysia, caused sapling density to decrease by 62% (Luskin et al., 2017), and the presence of pigs drove a shift in the plant communities toward more lianas and fewer trees compared with when vertebrates were excluded (Luskin et al., 2019). Trees are long-lived and experience very high mortality at early life stages, even in nondefaunated forests, so changes to early life stages often have negligible effects on overall population dynamics (Howe & Miriti, 2004). Effects on later life stages (i.e., saplings) should theoretically have stronger influences on population dynamics. Therefore, factors such as trampling, herbivory, and destruction of saplings may be very important, but they are difficult to consider in a global assessment of defaunation because the distribution of the animals that cause these effects and their foraging behaviors are highly variable across the world's tropical forests.

Although we attempted to design our analyses in a way that was biologically meaningful, our approach has several important limitations. First, we did not include density dependence. Many tropical trees experience very strong conspecific density or distance dependence, especially at early life stages (Comita et al., 2010; Harms et al., 2000; Lamanna et al., 2017), and density dependence is observed most strongly in seedlings (Song et al., 2021; Zhu et al., 2015). Although we incorporated these effects as differences in survival between undispersed and dispersed seeds and seedlings, population growth in our models was still exponential. However, because density dependence can keep populations in equilibrium, by not incorporating density dependence we may have actually overestimated how population growth rates would differ between defaunated and nondefaunated systems.

Second, the data we used are currently insufficient to quantify the (high) heterogeneity among real defaunated forests. Defaunated forests around the world vary in the severity of defaunation (how many species are extirpated) and the causes of defaunation (hunting, habitat loss, etc.) that determine which species are lost (Bogoni et al., 2022; Gallego-Zamorano et al., 2020). The effects of defaunation also depend on local animal communities and the interactions those animals have with plants. For trees, the population-level consequences of defaunation depend on factors such as the sensitivity of tree species to negative density dependence, seed defenses, and a host of other factors (Brodie et al., 2018). We tried to incorporate as much data as possible to account for the variability in global forest communities, but the fact that we did not detect a significant effect of defaunation on tree population dynamics may indicate that it is not currently possible to draw inferences on a global scale while ignoring the many important local factors.

Third, our approach cannot predict actual tree population dynamics in defaunated forests. The defaunation effects we collected from the literature were from studies of different species and at different sites than the demographic data to which we applied those effects. Of course, the population-level consequences of defaunation will vary according to local circumstances, and the demography of a species depends on many different biotic and abiotic factors that affect all life stages, making it difficult to isolate effects on particular life stages. Nevertheless, combining known defaunation effects with demographic data allowed us to explore the potential of defaunation to alter population dynamics across a range of tree life histories. Without considering how changes at specific life stages affect overall demography, it is impossible to determine the degree to which negative defaunation effects will actually imperil tropical plant communities. And, given the logistical difficulties of both measuring defaunation effects and monitoring whole-population demography, it is worth combining datasets to get a rough idea of what defaunation would mean for tree populations.

In our model, defaunation had almost no effect on population dynamics on average, but the tails of our results indicated that some species may be severely affected by defaunation. What explains how strongly defaunation affected the tree populations in our models? Most obviously, the parameter values drawn determined how defaunation affected λ. Greatly increased seed predation will negatively affect some tree populations, and greatly decreased seed predation will positively affect others. Similarly, some species will likely face catastrophic declines due to loss of seed dispersal, whereas other species will not be affected. Currently, there are no tools to identify which species will be affected in which ways. Besides parameter values, our results were influenced by the different life histories of the focal tree species. In our model, species that had low elasticities (how much a proportional change of one matrix element or vital rate affects λ) for seed survival or seedling survival had very small changes in λ regardless of parameter values, whereas species with high elasticities at those stages were strongly influenced depending on the parameter values used. Longer-lived species tend to have lower elasticities at early life stages (Heppell et al., 2000; Silvertown et al., 1993), meaning that long-lived species are theoretically less sensitive to defaunation effects at these stages. In contrast, shorter-lived species are more strongly influenced by changes at early life stages, meaning that, assuming identical defaunation effects, defaunation could more strongly affect these species.

In summary, given what is known about the effects of defaunation, what can be predicted about cascading consequences for tropical trees? Prior studies of individual species show that defaunation can cause significant population declines (Culot et al., 2017; Rogers et al., 2017), but it remains difficult to generalize across species and systems. Though knowledge is still limited, we attempted to bring together the best available data to address this important issue. Our results indicated that population declines may be less common than had been thought previously, meaning dispersal limitation may not cause the widespread, near-term species turnover that has been predicted to cause massive carbon loss. Although reduced species richness and changes in species composition have been observed in defaunated forests (Kurten & Carson, 2015; Nunez-Iturri et al., 2008), our results highlight that, given the current state of knowledge, how specific tree populations will respond to defaunation cannot be predicted. An improved understanding of processes such as seed predation, herbivory, and trampling may be key for understanding which species are affected by defaunation and how this scales up to community-level patterns of diversity.

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SUPPORTING INFORMATION

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

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