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RESEARCH ARTICLE

Effects of insect herbivory on seedling mortality in restored and remnant tropical forest

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Insect herbivory is one of the major drivers of seedling mortality in the tropics and influences plant abundances and community composition. Anthropogenic disturbance can alter patterns of insect herbivory with potential consequences on plant communities in restored forests. We planted seedlings of early- and later-stage successional tree species in 13–15-year-old restored and remnant tropical forests. We then either excluded insect herbivores or left seedlings exposed to examine how insect herbivory-affected seedling mortality. Early-successional seedlings experienced similar decreases in mortality when insect herbivores were excluded from both restored and remnant forest sites, but this effect was smaller and driven by only a few species in restored forests. Later-successional seedlings experienced a stronger decrease in mortality between open and insect-excluded treatments in remnant than restored sites. Our results suggest that herbivory-driven seedling mortality is lower in restored forests, particularly for later-successional seedlings. Results are encouraging from a restoration perspective because recruitment of later-successional seedlings is a key component of ecosystem recovery. However, if reductions in seedling mortality continue over the long term, this may affect tree community composition as succession progresses.

Key words: ecological restoration, fragmentation, plant-insect interactions, seedling survival, succession, tropical forest restoration

Implications for Practice

- Like in continuous forests, insect herbivory is an important biological filter of seedling establishment in restored and remnant forests within a deforested landscape.
- Lower seedling mortality of later-successional species in restored forests means practitioners can focus on alleviating non-herbivore sources of recruitment limitation.
- Long-term reductions in herbivory-driven seedling mortality could lead to dominance of some tree species and require management such as thinning of dominant species and enrichment planting of displaced species.

Introduction

Insect herbivory is a major cause of tree-seedling mortality in tropical forests (Clark & Clark 1985; Eichhorn et al. 2010; Hodkinson & Hughes 2012). Often, seedling mortality induced by insect herbivores is not uniform across tree species and populations due to the interaction between plant life-history strategies and insect herbivore diet breadth. For example, later-successional tree species with low fecundity and large seeds tend to be well protected from herbivory through greater concentrations of secondary chemical defenses (Poorter et al. 2004). In contrast, highly fecund, early-successional seedlings with small seeds typically invest less in secondary defenses and are therefore more susceptible to generalist insect herbivores (Coley 1983; Poorter et al. 2004). At the population level, specialist insect herbivory drives negative density and distance dependent seedling survival (Janzen 1970; Bagchi et al. 2014; Comita et al. 2014), conferring a rare species advantage by disproportionately killing abundant seedlings that recruit close to their mother trees (Wright 2002).

Insect herbivory is one of the key processes driving tree community composition in relatively undisturbed tropical forests (Harms et al. 2000; Levi et al. 2019). For example, Bagchi et al. (2014) found that the exclusion of insects in a biological reserve in Belize increased seedling abundance and shifted seedling community composition to favor small-seeded recruits compared to non-excluded plots. Similarly, Kursar et al. (2009) observed that congeneric coexistence of the diverse genus *Inga* in the Peruvian Amazon and Barro Colorado Island in Panama was driven by dissimilarity in antiherbivore traits.

Yet, a large percentage of tropical forests worldwide are highly fragmented or denuded (Arroyo-Rodriguez et al. 2017; Potapov et al. 2017; Chazdon et al. 2020). Evidence suggests

that forest fragmentation can lead to an overall decrease in insect herbivory (Arnold & Asquith 2002). For example, Fáveri et al. (2008) found that Amazonian trees in small fragments suffered lower herbivory than continuous forests, likely due to dispersal limitations of insect herbivores. Similarly, Chávez-Pesqueira et al. (2015) and Martinson and Fagan (2014) determined that insect herbivory decreased as fragmentation increased. Fragmentation can also reduce the abundance of insect herbivore specialists in habitat patches leading to increased insect herbivore diet breadth at the community level (Martinson & Fagan 2014; Rossetti et al. 2017). Altered plant–herbivore interactions due to fragmentation can lead to decreased plant beta-diversity between fragmented plant communities (Viswanathan et al. 2019).

Insect herbivory has been suggested as an important biological filter of tree-seedling recruitment and establishment in restored forests (Holl 2012), based on comparisons of percent herbivory by seedling successional stage (e.g. Mariano et al. 2018; Garcia et al. 2020), seedling herbivore defenses (Massad et al. 2011; Garcia et al. 2020), and factors influencing the biological control of insects in restored tropical forests (Roels et al. 2018). Reductions in herbivory and shifts toward herbivore generalism in degraded systems are predicted to affect tree community-composition (Chávez-Pesqueira et al. 2015; de Araújo et al. 2015a), potentially by releasing abundant tree species from density-dependent mortality that is driven by specialist insect herbivores (Pinho et al. 2017). However, no study has thus far investigated how insect herbivory directly affects the mortality of early and later successional tree seedlings in restored forests and the consequences for plant successional trajectories.

Understanding insect herbivory in degraded tropical systems becomes all the more salient considering the recent global commitments to hundreds of millions of hectares of forest landscape restoration (Chazdon et al. 2015). This global push to restore vast areas has come with a word of caution from restoration ecologists who have called for careful planning and understanding of processes that may affect the efficacy of restoration efforts (Palmer et al. 2016; Brancalion & Holl 2020).

Here, we test the effects of insect herbivory on tree-seedling mortality in remnant forest fragments and 13–15-year-old restored tropical forest at multiple sites in southern Costa Rica.

We used herbivore exclosures to compare the survival of planted tree seedlings of early- and later-successional species for 6–16 months. Specifically, we asked whether seedling survival was higher in exclosure treatments, and whether the magnitude of these differences changed with respect to forest type (restored vs. remnant forest fragments) and seedling successional stage (early vs. later) and consider the implications of the results for longer-term forest recovery in these restored sites.

Methods

Site Description

We conducted this study within a highly fragmented landscape in southern Costa Rica (Coto Brus, Puntarenas Province) (Fig. 1A) which has experienced a 70% decline in forest cover over the last 70 years (Zahawi et al. 2015). Remnant forest patches are interspersed among horticulture, agriculture, and grazing activities. The study area is considered a premontane tropical forest receiving 3,500–4,000 mm of precipitation per year and ranging from ~1,100 to 1,200 m in elevation.

We established our herbivory exclusion treatments in seven restored forest sites (hereafter "restored forests") that were previously used for pasture and/or mixed agricultural land and three remnant forest fragments ("remnant forests") (Fig. 1B). Each 0.25-ha restoration plot was established between 2004 and 2006 and separated by a minimum of 1 km (Holl et al. 2020). Plots were planted with 1,250 trees ha^{-1} which included equal proportions of two native species (*Terminalia amazonia* and *Vochysia guatemalensis*) and two fast-growing, naturalized species with N-fixing mutualisms (*Erythrina poeppigiana* and *Inga edulis*). In the 13–15 years between planting and the initiation of this study, restored forests experienced high levels of natural recruitment of native, early- and late-successional tree species, many of which are animal dispersed (Holl et al. 2017). A number of the early-successional recruited trees had matured sufficiently to contribute to the tree canopy and reproduce. Remnant forests were located within 5–50 m of restored sites. While susceptible to edge effects and somewhat disturbed by past selective logging, these fragments are representative of the remaining forest in much of Central America.
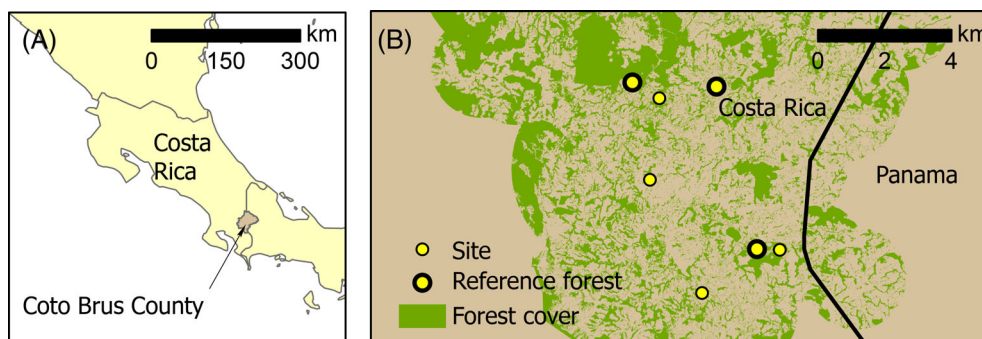

Figure 1. (A) Study region and (B) distribution of restoration sites across landscape. Sites with circles were paired with remnant forest plots. Adapted from Holl et al. 2020.

Species Selection

We examined seedling mortality of four early- and four later-successional tree-seedling species that are abundant in the study area (Table 1). All tree species are hereafter referred to by their generic names. We define early-successional species as pioneers that commonly establish after a major disturbance such as in an abandoned agricultural field. We consider later-successional species as those that are found either in the understory of mature forests or a mix of mature and secondary forests but that do not establish during the earliest stages of succession. Successional status was determined by a local botanist through literature reviews and extensive experience in this study system. Seeds were gathered from the landscape surrounding the study region from three to six mother trees for each species. Seeds of *Conostegia*, *Senna*, *Calophyllum*, *Otoba*, and most *Erythrina* were germinated and grown in open-air nurseries until they were 5–10-cm tall and then planted into plots. We planted *Senna* seedlings at two different times during the experiment, and monitored these plantings for 6 and 13 months, respectively; seedlings from both plantings were combined for analyses. We directly seeded *Pseudolmedia* into plots due to slow germination and measured mortality after germination. We transplanted *Croton* and *Allophylus* into experimental plots from three and five sites in the surrounding landscape respectively. Due to a shortage of reared seedlings in one restored plot, we collected ~20 naturally recruited *Erythrina* seedlings of similar size to nursery-grown seedlings from within the plot and combined them with reared seedlings for planting.

Experimental Design and Data Collection

In August 2017, over a decade after sites were originally planted, we placed four sets of two 1-m^2 quadrats at least 10 m apart and 5 m from the forest edge in each of seven restoration plots and three remnant forests (hereafter referred to as "forest type"). In each set, we randomly assigned quadrats as either open (exposed to insect herbivores) or exclosure (herbivores excluded) treatments. Insect herbivores were excluded by erecting a 1 × 1 × 1-m rebar frame with a ~1 × 1.5-mm porosity fiberglass screening covering over the frame. The screening was buried on all sides to prevent herbivores >1.5 mm in diameter from entering. A Velcro seam on one side of the exclosure allowed access for planting and sampling during the experiment.

We recognize that exclosures could have also prevented herbivory by vertebrates but herbivores such as tapirs have been extirpated from the landscape and livestock are excluded by barbed-wire fences at all sites. Also, the most abundant rodents in the sites (agoutis and squirrels, Joyce unpublished data) are granivorous so we expect they contributed little if any to herbivory. Finally, the patterns of herbivory we observed on plants before mortality were characteristic of insect folivores; namely caterpillars, orthopteroids, and leaf beetles, which produce damage that is easily discernable from vertebrate herbivory. Thus, we expect the vast majority of herbivory was caused by insects.

Open herbivory treatments included similar structural frames but with fiberglass screening that only covered the top and ~30 cm of upper sides to reduce litter fall and create similar light levels as the exclosure treatments. Open herbivory controls also had a 40-cm high barrier on the uphill side to block sliding debris, although a small amount of debris was still able to enter the open treatments located on steep slopes. As a result, we measured the steepest slope at 10 m uphill from each open treatment as this area accounted for the most debris. We then tested whether slope, forest type, and their interaction affected seedling mortality using a generalized linear model with a binomial distribution fit with penalized quasi-likelihood. As no slope effect was found, nor an interaction with slope and forest type on seedling mortality, we removed slope from subsequent models.

Before the experiment, we tested the extent to which the fiberglass screening reduced photosynthetically active radiation (PAR) using a LI-COR 1400. We found that the screening reduced PAR by ~35% compared to no screening. Despite reductions in PAR, the areas within our structures (screened) and adjacent non-screened areas experienced a similar number of sunflecks exceeding 100 μmol m^{-2} s^{-1}. These sunflecks play an essential role in tropical seedling growth in the understory (Chazdon & Pearcy 1991) and, given that several tropical seedling species in our study area experience asymptotic CO_2 uptake in the forest understory at very low light levels (~100–250 PAR) (Loik & Holl 1999), we were confident that light reductions would not compromise this study. We also measured canopy cover at each subplot in all restored and remnant forests using a densiometer. We used a linear model to compare canopy cover by forest type and found no difference between forests so we therefore do not include canopy cover in subsequent models.

Table 1. Seedling species used in the exclosure study indicating successional stage, sample size at the plot level, and monitoring period. Variable monitoring period in *Senna papillosa* is due to two separate plantings during the experiment. Variable monitoring period and sample size in *Pseudolmedia mollis* represents different rates and success of seed germination.

Species	Family	Successional Stage	Sample Size	Monitoring Period (Months)
Erythrina poeppigiana (Walp.) O.F. Cook	Fabaceae	Early	32	9
Conostegia xalapensis (Bonpl.) D. Don ex DC.	Melastomataceae	Early	32	15
Croton draco Schltdl. & Cham.	Euphorbiaceae	Early	32	7
Senna papillosa (Britton & Rose) H.S. Irwin & Barneby	Fabaceae	Early	128	6 or 13
Allophylus psilospermus Radlk.	Sapindaceae	Later	32	7
Calophyllum brasiliense Cambess.	Calophyllaceae	Later	24	6
Otoba novogranatensis Moldenke	Myristicaceae	Later	24	72
Pseudolmedia mollis Standl.	Moraceae	Later	24–47	3–13

Before planting, we cleared all living vegetation from within quadrats to minimize competition effects and ensure that herbivores were not hidden in vegetation inside exclosures. We then planted seedlings into herbivory treatments as they became available in August 2017, July 2018, and June 2019, and monitored seedling survival monthly for 6–16 months, depending on the species (Table 1). Seedlings were planted systematically following the same predetermined configuration in each quadrat. Quadrats were cleared of newly established, non-planted vegetation as needed throughout the study.

Data Analysis

We used a parametric survival analysis with right censoring to examine the effects of forest type (restored vs. remnant), herbivory treatment (exclosure vs. open), seedling successional stage (early vs. later) and their interactions on seedling mortality (Table S1, Supporting Information). We used an accelerated failure time (AFT) model to acquire coefficient estimates and test hypotheses. We conducted a priori tests of different distributions fit to our data using the *flexsurvreg* function in the R package *flexsurv* (Jackson 2016). We then compared the fit of different distributions using visual inspections of predicted vs. observed survival curves and log-likelihood. We chose the log-logistic distribution for our models because it had the lowest log-likelihood and provided the best fit when examining survival curves. To check the fit of our fully specified model with all covariates, we overlaid the predicted survivorship curve of the extreme value distribution vs. Kaplan–Meier (KM) curves of model residuals, which indicated a reasonable model fit. We also used separate AFT models with log-logistic distributions to test how survival of each individual species was affected by exclosure treatment in each forest type. We used the function *survreg* in the R package *survival* (Therneau & Grambsch 2000) to fit all models. We tested hypotheses regarding the effects of predictor variables and their interactions using

likelihood ratio tests based on comparisons of χ^2 distributions between full vs. reduced models. All analyses were conducted in R v.3.6.3 (R Core Team 2020).

Results

Main effects from our AFT model (Table S1) indicated a 34% faster time-to-seedling-death in open compared to exclosure treatments across both restored and remnant forest sites and early- and later-successional seedlings (AFT estimate = −0.42, CI [−0.55, −0.29], $p < 0.001$; Fig. 2A). Mean percentage of surviving seedlings at the end of the experiment was $67 \pm 29\%$ for exclosure and $55 \pm 29\%$ for open treatments. Early-successional seedlings had 156% faster time-to-seedling-death than later-successional seedlings across both forest types and treatment levels (AFT estimate = 0.94, 95% CI [−0.98, −0.09]; Fig. 2B). Mean percentage of surviving seedlings at the end of the experiment was $43 \pm 29\%$ for early-successional seedlings and $80 \pm 13\%$ for late successional species. Our model (Table S1) indicated a significant three-way interaction between forest type, herbivory treatment, and seedling successional stage with later-successional seedlings experiencing higher survival in exclosure ($78 \pm 8\%$ survival) compared to open treatments ($57 \pm 14\%$), but only in remnant forests (Fig. 3B). In restored forests, later-successional seedlings experienced only slightly (7%) higher survival in exclosure treatments ($p = 0.004$; Fig. 3B). In contrast, the net increase in early-successional seedling survival in exclosure compared to open treatments was 13–14% greater in both remnant and restored forests (Fig. 3A).

Individual species showed similar trends to full models but also revealed species-specific responses to exclusion treatments (Fig. 4, Table S2). In remnant forests, all species, except for *Allophylus* and *Calophyllum*, showed significantly lower survival in open than exclosure treatments. In restored forests, all species except *Allophylus*, *Calophyllum*, and *Pseudolmedia* had significantly lower survival in open than exclosure
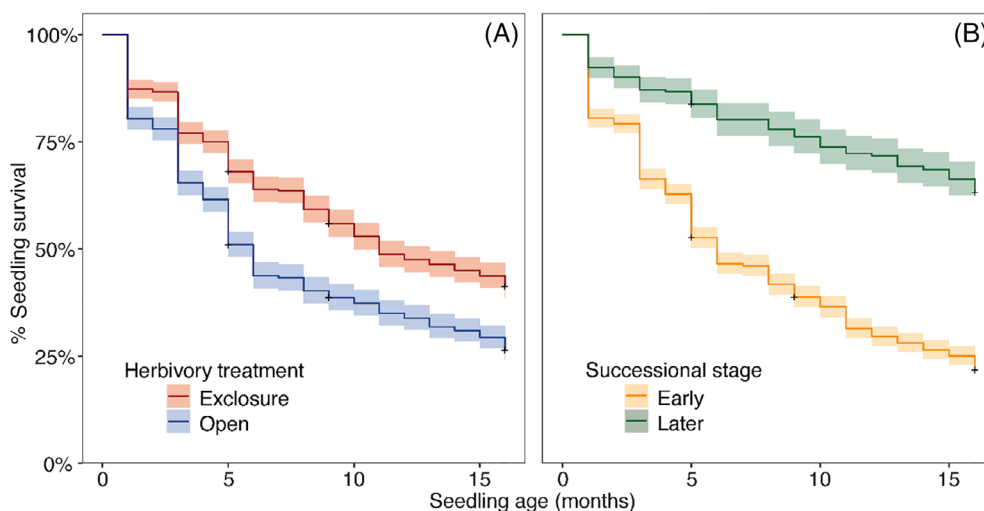

Figure 2. Kaplan–Meier curves showing survival in open and exclosure treatments (A) and early- and later-successional species (B) across both herbivory treatments and forest types. Shaded areas represent 95% CI.
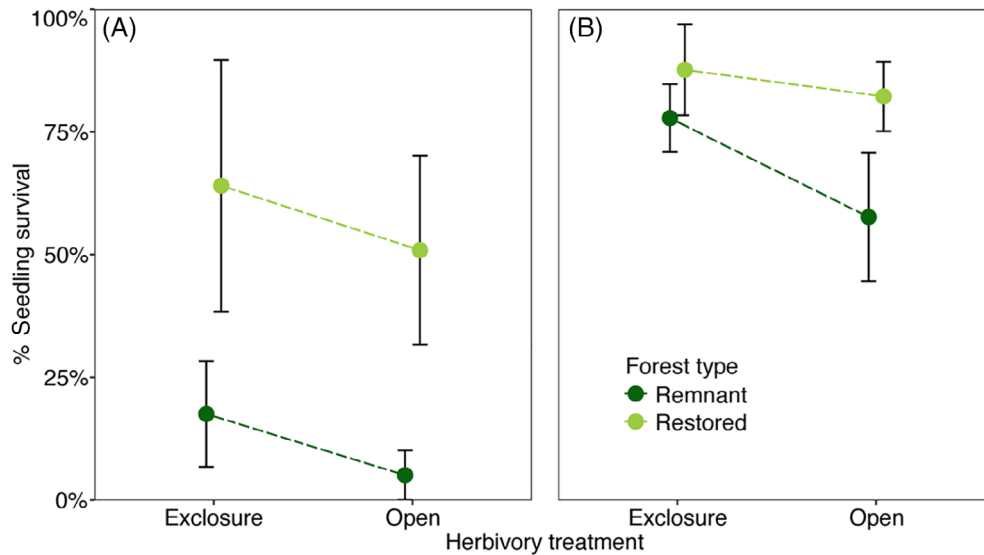
Figure 3. Survival in open vs. exclosure treatments by forest type for early- (A) and later- (B) successional seedlings. Values are means ±1 SD at the plot level (*n* = 7 for restored forests, *n* = 3 for remnant forests). Dashed lines present to visualize interactions.
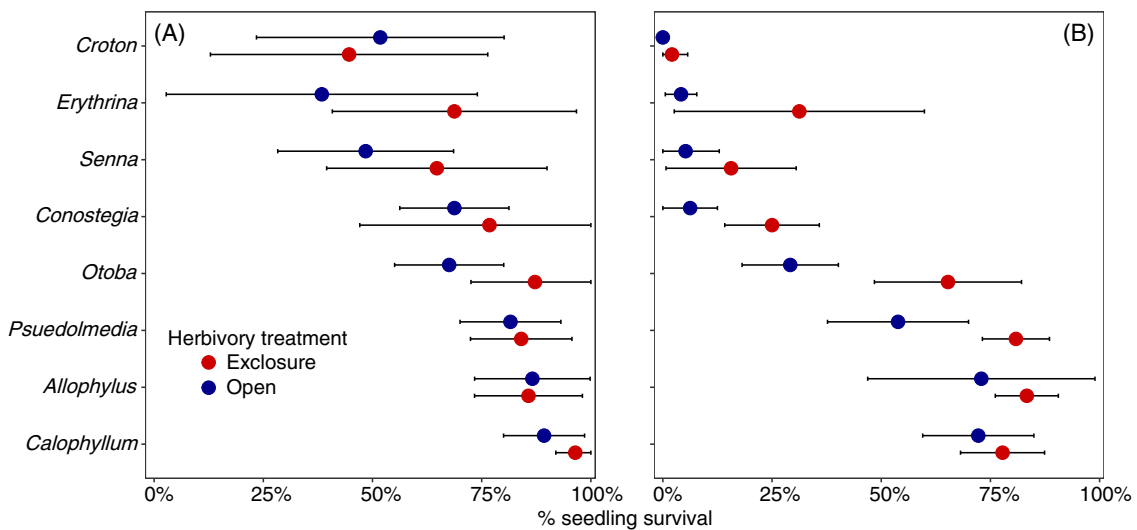

Figure 4. Species-specific seedling survival by herbivory treatment in restored (A) and remnant (B) forests. The top four species are early-successional and bottom four species are later-successional. Values are means ±1 SD at the plot level (*n* = 7 for restored forests, *n* = 3 for remnant forests).

treatments. Only one species, *Croton*, had significantly higher survival in open treatments but only in restored forests.

Discussion

We found that seedling survival was consistently lower in open compared to exclosure treatments. This suggests that insect herbivory is a major factor driving seedling mortality in both remnant and restored forests, but the effect was more pronounced and less variable in remnant forests. Most species had much lower mortality in exclosure compared to open treatments in remnant forests, whereas the trend in restored forests appeared to be driven by only

a few key species suggesting that seedlings in restored forests experience less insect-herbivore pressure than remnant forests in our study region. The difference in magnitude of herbivore-induced mortality between forest types was seen in both early- and later-successional species. It is therefore unlikely this effect was purely due to tightly coevolved relationships between herbivore and plant communities consistent with Whitfeld et al. (2012). For example, the early-successional species *Conostegia xalapensis* recruits abundantly in restored forests but is almost never found in remnant forests. Yet, *C. xalapensis*, still experienced much higher mortality in open than exclosure treatments in remnant forests. This suggests that differences in mortality

between treatments in remnant forests are driven more by overall higher herbivory levels as opposed to resource tracking by specialist herbivores.

While to our knowledge no other studies have compared the effects of insect herbivory on plant survival in restored and remnant forests, our results concur with studies reporting that herbivory decreases in small fragments (Ruiz-Guerra et al. 2010; Chávez-Pesqueira et al. 2015). However, our study contrasts with evidence indicating strong increases in herbivory at forest edges (Benitez-Malvido et al. 2016), which is somewhat surprising given that our restoration plots are small and have large edge-to-interior ratios. Results are encouraging from a restoration perspective, as it appears that our restored forests experience little spillover of destructive, hyper-generalist insect herbivores, such as large grasshoppers that are abundant in the surrounding matrix (Kulikowski personal observation) and can dominate edge habitats (Wirth et al. 2008; De Carvalho Guimaraes et al. 2014).

Like other studies that have examined seedling susceptibility to insect herbivory (Davidson 1993; Poorter et al. 2004; Mariano et al. 2018), we found that early-successional species suffered higher overall mortality than later-successional species. Lower survival rates of early-successional species have been attributed low investment in antiherbivore secondary chemicals (Hanley 1998). However, we observed far higher mortality of early-successional seedlings in remnant compared to restored forests in both open and exclosure herbivory treatments. Factors such as differences in pathogen load (Augspurger 1984; McCarthy-Neumann & Kobe 2008) or microclimatic variation (Bazzaz & Pickett 1980) between forest types may have contributed to these disparities in survival. Even though canopy cover was similar between restored and remnant forests, subtle differences in light quantity and quality that cannot be detected by densiometer readings could have contributed to survival disparities between forest types.

Later-successional seedlings were more susceptible to insect herbivory in remnant than restored forests, consistent with other studies showing lower herbivory in early- than late-successional systems (Silva et al. 2012; Neves et al. 2014). Restored forests containing only a small portion of the regional plant diversity may therefore experience less herbivory from specialist herbivores due to decreased host-plant availability. This is similar to fragmented systems (Holt 2009; Bagchi et al. 2018) where reduced plant resources may be responsible for shifts toward generalist herbivores and less herbivory than continuous forests (Martinson & Fagan 2014; de Araújo et al. 2015b; Rossetti et al. 2017; Souza et al. 2019). However, richness and abundance of later-successional species should increase as succession continues. Therefore, potential differences in herbivory between restored and remnant forests may be a product of forest age, and if plant communities continue to recover, so may their respective herbivores, though effects may not be seen for decades (Dent et al. 2013).

Restored forests varied substantially with respect to isolation from larger patches of remnant forests in the landscape (Kulikowski 2020). Martinson and Fagan (2014) found that isolation of habitat patches negatively affected specialist insect herbivory. It is therefore possible that differences in seedling survival between restored and remnant forests are explained by herbivore dispersal limitation which, unlike the recovery of plant resources, could persist for many years leading to depauperate herbivore communities. Such losses of mammalian herbivores in other tropical systems have led to the release of some tree species from density-dependent survival (Kurten 2013; Camargo-Sanabria et al. 2015).

In conclusion, we show that insect herbivory strongly influences tree-seedling mortality in a highly fragmented landscape typical of much of the tropics. Further, later-successional seedlings in restored forests showed a weaker response to herbivory than those in remnant forests. This result extends previous theoretical and empirical work to a restoration context, suggesting that the potential for decreased insect herbivory and herbivore specialism in fragmented landscapes differentially affects restored vs. remnant forest fragments. As such, our results represent a double-edged sword for tropical restoration. On the one hand, it is encouraging that insect herbivory somewhat spared later-successional species in our restored forests, which is likely to have positive effects on ecosystem recovery. But should the lack of insect-herbivore pressure continue as forests age, restored forests may be susceptible to biotic homogenization due to the breakdown of diversity-driving mechanisms like density-dependent seedling mortality caused by insect herbivore specialists. If such a breakdown was revealed to widely affect restored tropical forests, restoration practitioners would need to consider strategies that allow for changes in relative plant abundances, such as thinning of dominant tree species and/or enrichment planting of desirable species.

Acknowledgments

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Output and structure of mixed-effects Cox proportional hazard model predicting seedling mortality by herbivory treatment (open vs. exclosure), forest type (restored vs. remnant), and successional stage (early vs. later).

Table S2. Results of separate loglogistic AFT models for each seedling species by forest type.