RESEARCH ARTICLE

Wildlife differentially affect tree and liana regeneration in a tropical forest: An 18-year study of experimental terrestrial defaunation versus artificially abundant herbivores

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Abstract

1 Hunting and land use change modify native herbivore abundances and cause cascading effects in natural ecosystems. The outcomes for vegetation depend on changes to specific plant–animal interactions, such as seed dispersal or predation, or physical disturbances.

2 We experimentally manipulated terrestrial wildlife populations in a primary lowland forest in Malaysia over an 18-year period (1996–2014) to understand how artificially high or low animal densities affect tree and liana regeneration. Our study site retains a diverse wildlife community and artificially high densities of native wild pigs (*Sus scrofa*) that are sustained by crop raiding in distant oil palm plantations. We used fencing that excluded terrestrial animals >1 kg to experimentally simulate conditions similar to those in defaunated forests. These two treatments – abnormally high pig abundances and megafauna loss from hunting – represent common outcomes in disturbed Southeast Asian forests and are characteristic of many forests globally. We focused on trees and lianas because they are the two dominant woody life-forms in tropical forests and crucial determinants of forest structure and function.

3 We found that liana sapling abundances (30–100 cm height) increased by 86% in unfenced control plots with wildlife but were stable in exclosures. In contrast, tree abundances did not change in unfenced control plots but increased by 83% in exclosures without wildlife. Evidence of scaring on surviving stems suggested that these inverted outcomes were driven by selective use of tree saplings for wild pig nests. Lianas may also have greater tolerance to wildlife disturbances like nest building. By the end of the study, lianas comprised 38% of all saplings in unfenced controls but just 14% in exclosures.

4 *Synthesis and applications*. We conclude that artificially abundant wildlife, such as crop-raiding wild pigs, may shift tropical forest understories towards lianas while defaunation may shift it towards trees. These results highlight that ecological cascades from hunting or land use change can alter plant functional types and reshape to long-term patterns of forest succession and change. Managing unnatural wild boar populations may be required to conserve native plant communities in both their native and exotic ranges.

1 | INTRODUCTION

Hunting and agricultural expansion cause widespread distortion of wildlife communities, especially in the tropics (Benítez-López et al., 2017). Both processes cause cascading impacts on the vegetation because wildlife play an important role in regulating plant population dynamics through seed predation, seed dispersal and herbivory (Beck, Snodgrass, & Thebpanya, 2013; Estes et al., 2011; Taber et al., 2016; Wright, 2003). The types of cascading effects depend on the affected animal's ecology, such as whether they are seed dispersers or predators, and the specific plant traits, such as whether they are dispersed by vertebrates (Jia et al., 2018). While altered wildlife communities can shift both the composition and functional traits of the plants (Dirzo et al., 2014), the specific outcomes are contingent on the ecology of local fauna and flora and will vary between sites and between differences types of disturbances.

The links between animals and plants are most apparent when herbivores are hunted to local extinction, reducing plant consumption (Dirzo et al., 2014; Jia et al., 2018). However, hunted sites often first lose their predators, and this releases herbivore populations that are then able to overconsume plants (a 'trophic cascade'; Estes et al., 2011; Michel & Sherry, 2012; Taylor, Ryan, Brashares, & Johnson, 2016). A notable example are the high densities of white-tailed deer in some wolf-free American forests, which have suppressed tree regeneration (Rooney & Waller, 2003). Herbivore populations can also balloon if they are subsidised by food from humans (Oro, Genovart, Tavecchia, Fowler, & Martínez-Abraín, 2013). Our recent work at the Pasoh Forest Reserve in Peninsular Malaysia, for example, illustrated that artificially high densities of native wild pigs (*Sus scrofa*, the common name is "wild boar") are sustained by their crop-raiding in nearby oil palm plantations (Luskin et al., 2017). Pasoh's wild boars then strongly reduced tree sapling abundance in adjacent primary forests. This creates two common ecological cascade typologies in disturbed forests globally: (a) low herbivore abundances in hunted forests and (b) artificially high herbivore abundance where there are trophic cascades or food subsidies.

We manipulated large terrestrial wildlife densities over two decades (1996–2014) in the Pasoh forest of Malaysia and assessed changes to the understory tree and liana community. Specifically, we wanted to understand trade-offs in tree and liana regeneration under two conditions: (a) the absence of large wildlife, where we used experimental fenced areas to simulate conditions in defaunated forests, and (b) the sustained presence of artificially high densities of wildlife, which was represented by unfenced control plots where wild boars were common. We focused on trees and lianas because they are the two most important life-forms in tropical forests. Lianas constitute as much as 20%–25% of tropical woody species diversity, store 10%–20% of above-ground biomass, provide food resources for wildlife, and suppress the growth and survival of trees (DeWalt et al., 2015; Schnitzer & Bongers, 2002). A growing body of research also suggests that there are increasing abundances of lianas in Neotropical forests caused by the loss of seed dispersing vertebrates (Bello et al., 2015; Brodie & Gibbs, 2009; Campbell, Laurance, & Magrach, 2015; Laurance et al., 2014; Osuri et al., 2016; Peres, Emilio, Schietti, Desmoulière, & Levi, 2016; Wright, Hernandéz, & Condit, 2007; Wright, Sun, Pickering, Fletcher, & Chen, 2015). Changes in the relative abundances of trees and lianas can affect plant diversity and ecosystem functioning. A notable example is that increases in the relative abundances of lianas versus tress can reduce forest carbon sequestration because lianas have less wood volume and lower wood density than trees (Osuri et al., 2016; Peres et al., 2016).

While this paper investigates the impact of large terrestrial wildlife in general, our study may be particularly relevant for understanding the long-term impacts of abundant wild boars in the region and globally. Wild boars are the dominant large vertebrate at Pasoh and similar oil palm landscapes that now cover Southeast Asia's lowlands (Ickes, 2001; Luskin, Christina, Kelley, & Potts, 2014). In forests remaining in oil palm landscapes, sustained high wild boar densities coincide with plentiful fruit availability in the adjacent oil palm plantations (Luskin et al., 2017). Wild boars have been found to cause extensive damage to regenerating tree and liana seedlings and saplings through trampling, soil disturbance and harvesting for nest-building (Luskin et al., 2017). During the decades that oil palm is fruiting and wild boars are artificially abundant in nearby forests, their harvesting of woody stems for birthing nests may exceed 170,000 tree and liana seedlings and saplings per year over an area of 2 km^2 (Ickes, Paciorek, & Thomas, 2005; Ickes & Thomas, 2003). Similar ecological consequences of wild boar may also become important in their introduced range, especially in areas of Neotropics where their abundances have rapidly increased in recent decades (Pedrosa, Salerno, Padilha, & Galetti, 2015).

Our study design was thus informed by expected differences in how wild boar nest building might differentially affect trees and liana saplings. Specifically, we first hypothesised that there is apparent competition between trees and lianas that is mediated by their shared predator, wild boars. As such, we predicted that a decline in either trees or lianas would allow populations of the other plant functional group to increase (a compensatory effect). Second, we predicted that both trees and lianas would have lower abundances in open controls due to higher seed, seedling, and sapling mortality from wildlife. Third, we predicted the flexible biomechanical properties of lianas make them more resistant to breakage than tree

stems which reduces their vulnerability to trampling or nest building (Putz & Mooney, 1991; Rosin, Poulsen, Swamy, & Granados, 2017; Terborgh et al., 2016).

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted within the 600-ha primary forest stand of the 1,840-ha Pasoh Research Forest (hereafter Pasoh; 2°58′47′N, 102°18′29′E) in Negeri Sembilan, Peninsular Malaysia. Pasoh is surrounded on three sides by monoculture oil palm plantations that extend for 4–10 km away from the reserve. On the fourth side, Pasoh is connected to more extensive network of logged forest (Luskin & Potts, 2011). Pasoh has been a focal site of tropical forest research in Southeast Asia since 1975, including a 50-ha forest dynamics plot that has been monitored since 1985.

The 50-ha plot includes 816 species of trees with dbh ≥1 cm. The canopy is 40–60 m tall and it is dominated by emergent and canopy trees of Dipterocarpaceae (Davies, Noor, LaFrankie, & Ashton, 2003). The reproductive phenology at Pasoh exhibits supra-annual general flowering and mast fruiting (GFMF). Flowering occurs on intervals of 2–8 years, cued by drought and low temperature events (Chen et al., 2017). During the last 20 years, GFMF events were recorded in 1996, 2002, 2005, 2009, 2010, 2012 and 2014. There is abundant fruit during these periods and many animal populations quickly increase (Sun, Chen, Hubbell, Wright, & Noor, 2007). Tree stem abundances and basal area are dominated wind-dispersed species, especially trees in the Dipterocarpaceae family (Osuri et al., 2016; Seidler & Plotkin, 2006).

2.2 | Wildlife community

Pasoh retains an abundant and diverse wildlife community. The Eurasian wild boar (*S. scrofa*) has been the most common megafaunal species here since the early 1990s due to supplemental food (a resource subsidy) from fruit in the bordering oil palm plantations (Luskin et al., 2017). Primates, mouse deer, terrestrial and arboreal rodents, and porcupine have always been common at Pasoh and long-tailed and short-tailed macaques have always been very abundant. Recent work by the TEAM camera trapping network confirmed the most common species at Pasoh from 2012 to 2015 are macaque monkeys (*Macaca nemestrina* and *fascicularis* and wild pigs (Jansen, Ahumada, Fegraus, & O'Brien, 2014). Specifically, the 2012–2015 TEAM surveys found that the relative abundance index (RAI, measured as independent photos per 100 trap nights) was <2 for *Atherurus macrourus* (bushtailed porcupine), <2 for *Tapirus indicus* (tapir), <2 for *Muntiacus muntjac* (deer), and <3 for *Tragulus* species (greater and lesser mousedeer combined), 6.0 for *Macaca fascicularis*, 19.9 for *S. scrofa*, and 34.8 for *M. nemestrina* (all other species had RAI of <1 photo per 100 trap nights, J. Moore, personal communication; Beaudrot et al., 2016). Camera trapping has also recorded sambar deer, serow, Malayan sun bear, civets, leopards and clouded leopards. Elephant, rhinoceros and gaur were extirpated during the 20th century. There has been a sustained period of low-level hunting over the past two decades. The human population in the Pasoh landscape is dominated by Muslim inhabitants whose Halal diet does not incentive them to hunt pigs (Luskin et al., 2014). There is a Chinese minority who do hunt pigs and primarily hunt within oil palm plantations. In the non-Muslim areas of Southeast Asia, wild pigs are often hunted to extremely low levels (Harrison et al., 2016).

2.3 | Exclosure experiment

An exclosure experiment was established in 1996 along the southern edge of the 50-ha forest dynamics plot, 1.3 km from the nearest forest edge or plantation (Ickes, Dewalt, & Appanah, 2001). The exclosures replicates were spaced at 50 m intervals along a 400 m east-west transect. Eight 49 m^2 (7 × 7 m) open-top exclosures were constructed. Exclosure fences were made with 1.5 m tall, heavy gauge, 4 cm^2 mesh chain-link metal anchored by solid wood posts. The exclosures were designed to exclude terrestrial animals >1 kg (primarily wild boar, tapir, and several deer species), but allowed access by smaller animals (most rodents) as well as volant, arboreal and semi-arboreal animals that constitute most of the seed-disperser community (e.g., birds, primates, sun bear and civets).

Each 49 m^2 exclosure included a central 25 m^2 (5 × 5 m) vegetation monitoring plot and two 25 m^2 control plots (Figure S1). The controls were located 1 m outside the fences on the sides that most closely resembled the vegetation structure within the experimental plot in 1996 (Ickes et al., 2001). In 2014, we discarded one severely damaged exclosure and we recensused the remaining seven. Due to time constraints of our botanists in 2014, we recensused the full 25 m^2 exclosure plot and half of each 14 controls (12.5 m^2 in each). This provided seven replicates of one 25 m^2 exclosure plot and two 12.5 m^2 control plots.

2.4 | Monitoring long-term sapling dynamics

In August–September 1996 and August 2014, all woody stems above 30 cm height in all exclosures (n = 8) and adjacent control plots (n = 16) were tagged, identified as trees or lianas, and their heights were measured. Experienced field botanists could distinguish lianas versus trees from the slenderness of their stems and the initiation of the twining habit, in addition to genus and family level identification. Treatment effects on trees were reported by Luskin et al. (2017) with a focus on identifying changes in larger saplings (>1 cm dbh, generally >2.5 m height). In this study, we focus on smaller saplings and the differences between trees and lianas. None of the vegetation monitoring plots in the seven exclosures and associated control plots were in the vicinity of conspicuous canopy gaps.

2.5 | Measuring evidence of sapling damage by wildlife

Many tree and liana stems that are snapped by wild boar survive and initial resprouting was found to be similar between the two life-forms

(Ickes, Dewalt, & Thomas, 2003). We evaluated physical damage to woody saplings (30–100 cm height) by counting stem scars in 1996 and in 2014 (following Terborgh et al., 2016 and Luskin et al., 2017). Only full-circumference scars on the main stem were included as signs of stem breakage and subsequent recovery. This typically involved stem survival following complete snapping and removal of the stem by wild boar for nest building. Damage from fallen branches and canopy debris was assumed to occur equally in exclosures and controls.

2.6 | Statistical analyses

We used GLMMs to examine if the effects of plant life-form (trees vs. lianas), treatments (exclosures vs. controls) and census year (1996 and 2014) on the abundance of saplings, height of saplings and the number of stem-break scars. Pairs of exclosure and control plots were treated as a random effect in all models and the two 12.5 m^2 control plots that accompanied each exclosure were treated as a single 25 m^2 control plot to avoid pseudoreplication. GLMMs for abundance and stem-break scars were fit with Poisson distributions and GLMMs for height were fit with a Gaussian distribution (heights were log-transformed for normality). To assess significance in GLMMs with Gaussian distribution we used Satterthwaite approximations for the degrees of freedom (lmerTest package in R (Kuznetsova, Brockhoff, & Christensen, 2017). For GLMMs with Poisson distributions we used z value test statistics (glmm package in R Knudson, 2015). All statistical analyses were conducted using the statistical program R version 3.5.1.

3 | RESULTS

3.1 | Tree and liana abundance shifts

There were no significant differences in the abundance of tree or liana saplings between exclosures and controls in 1996 (Figure 1). In 1996 there were on average 56.4 tree and 16.6 liana saplings 30–100 cm height per 25 m^2 plot (Figure 2). Between 1996 and 2014, tree sapling abundance increased by 83% in exclosures ($p < 0.01$), but there was no significant change in tree sapling abundance in control plots ($p = 0.57$, Figure 1). In contrast, liana sapling abundances increased by 86% in controls ($p < 0.01$) but did not increase in exclosures ($p = 0.96$; Figure 1; Table 1). This resulted in a shift in life-form composition between the treatments: In 2014, there were 32.6 more tree saplings per 25 m^2 plot in exclosures than controls plots ($p < 0.01$), and there were 19.7 more liana saplings per 25 m^2 plot in controls than exclosures ($p < 0.01$). The initial relative abundance of lianas was slightly greater in controls (26.9%) than exclosures (20.01%; $p = 0.03$), but from 1996 to 2014, the relative abundance of liana saplings increased by 10.9% in controls and decreased by 6.2% inside exclosures (both $p < 0.01$; Figure 2).

3.2 | Sapling damage

The number of stem-break scars in 2014 depended on treatment, life-form and sapling size ($p = 0.013$ for the three-way interaction term;
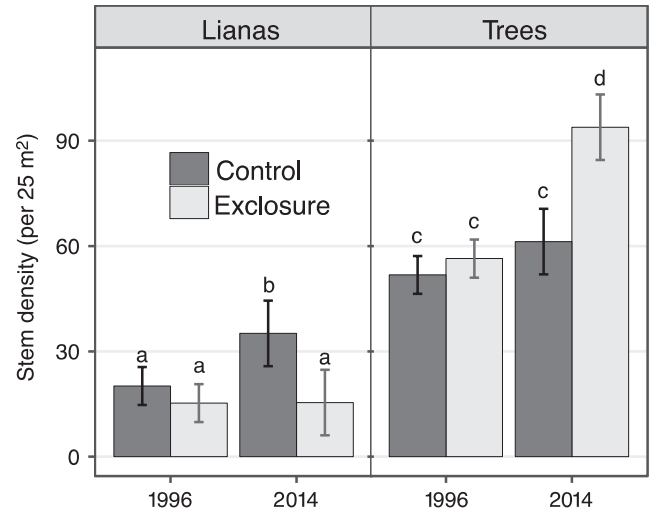

FIGURE 1 Sapling density (stems 30–100 cm height per 25 m^2 plot ± 1 SE) in open control plots and fenced wildlife exclosures in 1996 and 2014. Significant differences are indicated by different letters ($p < 0.05$)
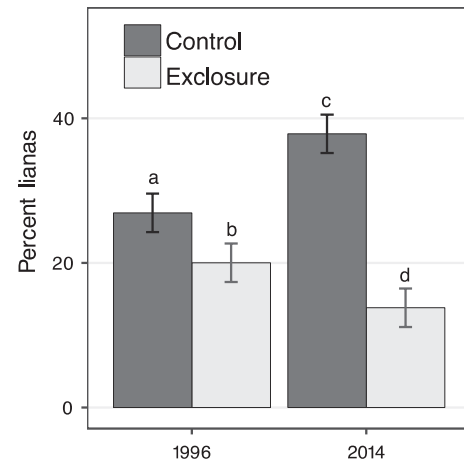

FIGURE 2 Relative abundance of liana saplings among all woody stems (per 25 m^2 plot ± 1 SE) in 1996 and 2014. Different letters indicate significant differences between controls (dark grey) and exclosures (light grey) in each year ($p < 0.05$)

Table 2). There were 47.49% and 49.99% fewer scars per stem for trees and lianas in exclosure plots than control plots, respectively (both $p < 0.01$; Figure 3). However, the percent of stems with one or more scars was 50.59% lower for trees in exclosures compared to controls ($p < 0.01$) but only 26.39% lower for lianas ($p = 0.236$). The number of stem-break scars was greater for larger saplings ($p < 0.001$; Table 2).

These results indicate that a higher percentage of trees were broken than lianas and that exclosures provided more protection for trees than for lianas.

3.3 | Sapling heights

From 1996 to 2014, the mean height of liana saplings increased by 5.29 and 8.21 cm in controls and exclosures, respectively, and the

TABLE 1 Predictors of sapling abundances (log-transformed) assessed using GLMMs. The significance table shows effects of exclosure treatment [Trt(EX)] relative to the control, Year (2014) relative to 1996, and tree life-form (T) relative to lianas. Interactions are shown with '×'

	Estimate	SE	Z	p
(Intercept)	3.75	0.10	35.88	<0.001
Trt(EX)	−0.83	0.10	−8.02	<0.001
Life-form (T)	0.03	0.08	0.40	0.688
Year (2014)	1.28	0.06	19.80	<0.001
Trt(EX) × Life-form (T)	0.43	0.14	3.18	0.001
Trt(EX) × Year (2014)	0.21	0.12	1.83	0.067
Year (2014) × Life-form (T)	−0.58	0.09	−6.10	<0.001
Trt(EX) × Year(2014) × Life-form (T)	0.75	0.15	4.87	<0.001

TABLE 2 Factors affecting the number of stem-break scars on saplings in 2014, assessed using GLMMs. The table shows effects of treatment [Trt(EX) denotes exclosures relative to controls], lifeform [Life-form (T) denotes trees relative to lianas] and stem height (cm, log-transformed). Height was included because taller stems have the potential to show more scars

	Estimate	SE	Z	p
(Intercept)	−0.77	0.15	−5.06	<0.001
Trt (EX)	0.56	0.38	1.48	0.138
Life-form (T)	0.30	0.17	1.78	0.075
Height	0.17	0.04	4.45	<0.001
Trt(EX) × Life-form(T)	−1.02	0.41	−2.51	0.012
Trt(EX) × Height	−0.17	0.09	−1.77	0.076
Life-form (T) × Height	−0.06	0.04	−1.45	0.146
Trt(EX) × Life-form(T) × Height	0.25	0.10	2.48	0.013

TABLE 3 Predictors of sapling stem heights (log-transformed), assessed using GLMMs. The significance table shows effects of exclosure treatment [Trt(EX) relative to controls), Year (2014) relative to 1996, and tree life-form (T) relative to lianas. Interactions are shown with '×'

	Estimate	SE	t-value	p
(Intercept)	3.90	0.06	66.1	<0.001
Trt(EX)	0.04	0.09	0.4	0.655
Life-form (T)	0.68	0.06	12	<0.001
Year (2014)	0.26	0.07	3.7	<0.001
Trt(EX) × Life-form (T)	−0.05	0.10	−0.5	0.615
Trt(EX) × Year (2014)	0.30	0.12	2.5	0.012
Year (2014) × Life-form (T)	−0.50	0.08	−6	<0.001
Trt(EX) × Year(2014) × Life-form (T)	−0.16	0.13	−1.2	0.239

FIGURE 4 Height size-class distribution of all tree and liana saplings (30–100 cm height) in control and exclosure plots in 1996 and 2014. Each set of bars denotes a 14 cm size class covering the range from 30 to 100 cm in height
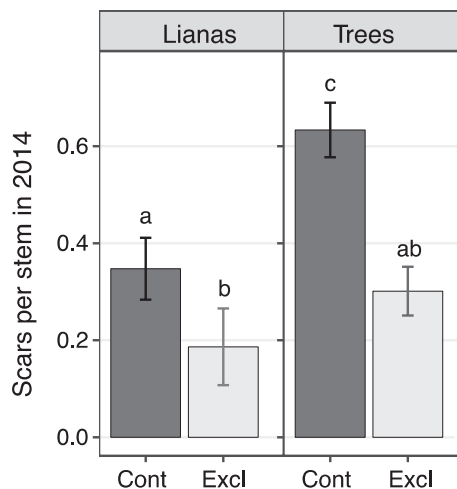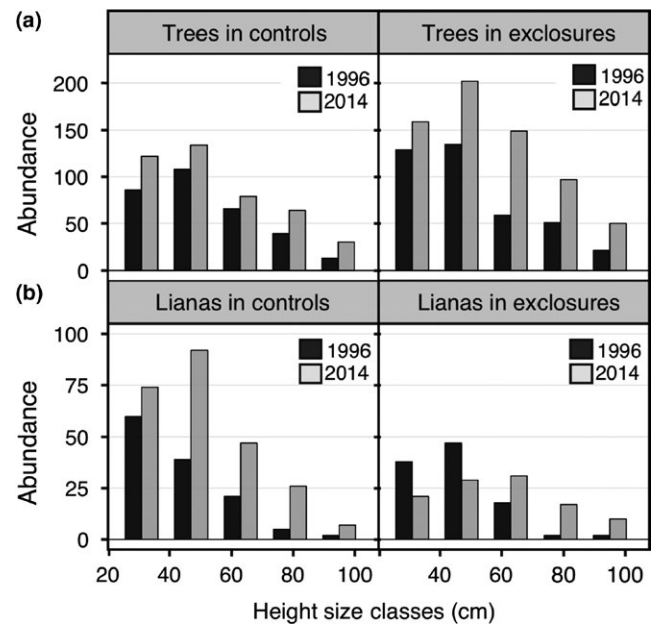

FIGURE 3 The mean number of stem scars per individual sapling (30–100 cm height) resulting from breakage and subsequent recovery. Different letters indicate significant differences between liana and tree seedlings in controls (dark grey) and exclosures (light grey; p < 0.05)

mean height of tree saplings increased by 2.55 and 3.96 cm in controls and exclosures, respectively. Significant interactions for treatment × year and year × life-form in the GLMM indicated that mean sapling height was significantly greater inside exclosures in 2014, and significantly greater in trees than lianas in 2014 (Table 3, Figure 4). The height distributions for both tree and liana saplings significantly changed between 1996 and 2014 for trees and lianas in exclosures and lianas in controls (Kolmogorov–Smirnov test, p < 0.01) but not for trees in controls (KS test, p = 0.18). For trees in exclosures, the abundance of stems in all size classes increased from 1996 to 2014, indicating higher recruitment and survival. However, as seen in the histogram in Figure 4 in which the saplings are split into five 14 cm

size classes, liana abundances in exclosures decreased for the smaller two size classes (30–58 cm) and increased for the larger three size classes (59–100 cm). This suggests lianas in exclosures faced comparatively lower recruitment but higher survival.

4 | DISCUSSION

We observed differential effects on the regeneration of tree and liana saplings under artificially high and low native wildlife abundances. This suggests wildlife play an important role determining the plant functional traits of Malaysian rainforest understories. Over the 18-year study period, the number and relative abundance of liana saplings doubled in the presence of sustained high wildlife densities. The high wildlife densities were driven by food subsidies to wild boars from oil palm plantations located 1.3 km away from the exclosure experiment, and this is a common issue for many remaining forests in the region (Luskin et al., 2014, 2017). In contrast, in the experimental defaunation treatments where terrestrial wildlife was excluded by fences, tree sapling densities nearly doubled and the relative abundance of lianas was halved. The exclosure treatment recreates conditions in hunted forests that are also common in the region (Harrison et al., 2016). Our results demonstrate that wildlife can play a key role mediating tree and liana regeneration in tropical forests. Our study also highlights that both artificially high and low wildlife abundances from crop raiding and hunting, respectively, may shift the functional composition of tropical forests.

4.1 | Apparent competition between trees and lianas

Lianas may have been indirectly facilitated by reduced apparent competition with tree saplings in controls. First, the divergent trajectories of liana and tree saplings in unfenced controls and fenced exclosures at Pasoh are likely explained by the direct and indirect effects of wild boar (*S. scrofa*), which is the most abundant large animal in the region (Ickes, 2001; Luskin et al., 2014, 2017). Wild boars harvest enormous quantities of saplings for nest-building at our site (Ickes et al., 2003). This study confirms how this disturbance may drive important cumulative effects on forest composition, by disproportionately suppressing tree saplings, which showed higher rates of scars than lianas. The biomechanics of flexible liana stems may make them more difficult to break or uproot (Putz & Mooney, 1991). If this provides greater resilience to disturbances, it can help lianas indirectly out-compete trees in the presence of wildlife. Browsing or trampling by other common terrestrial wildlife such as deer and tapir may have also contributed to reducing tree sapling densities in unfenced areas. For example, damage by animals other than nest-building wild boars was also shown to be an important cause of seedling mortality in Neotropical, Afrotropical, and Bornean forests (Rosin et al., 2017). The relative importance of consumptive versus non-consumptive wildlife impacts in tropical

forest understories, and which species plant key roles, requires more research.

Lianas in our study may have also benefited from altered microhabitats created by wildlife disturbances. Exclosures experiments in grasslands show the indirect role of herbivores in shaping plant composition via increasing ground light levels, because browsing on taller stems opens up the grassland canopy (Borer et al., 2014). We suspect this same mechanism is partially responsible for the superior performance of lianas in control plots in our study. The removal of large numbers of tree saplings by wild boar produced higher light levels in unfenced controls. Since many liana species are light demanding and prefer disturbed areas, they may benefit from a more open understory created by pigs (Campbell et al., 2015). Targeted experimental work to quantity the indirect effect of wildlife in mediating ground light conditions and its influence on plants is underway at our study site.

4.2 | Long-term effects on plant communities

Unnatural wildlife densities produce important changes to plant communities. First, wild boar were determined to be the main cause of a 62% decline in the abundance of 1–1.5 cm dbh tree saplings from 1986 to 2010 in the Pasoh 50-ha Forest Dynamics Plot (Luskin et al., 2017). Second, the tree community diversity at Pasoh significantly increased over same period for saplings 1–10 cm dbh. We have yet to see shifts in tree stem classes >10 cm dbh and a recent study of canopy lianas at Pasoh did not detect significant changes from 2000 to 2014 (Wright et al., 2015). Longer monitoring may show that the understory vegetation changes observed in our study become reflected in the canopy, but it takes many decades for most trees and lianas to grow into the canopy. Alternatively, altered understory plant composition may not result in altered canopy plant composition if wildlife effects simply replace some of the mortality that would have occurred through self-thinning. Other mechanisms may also be important in explaining survival and persistence of canopy lianas and trees, such as periodic droughts that are unrelated to wildlife (De Deurwaerder et al., 2018). Further monitoring of liana and tree dynamics in relation to both abiotic and biotic drivers will help resolve what factors interact with herbivores to maintain functional diversity in this forest.

4.3 | Generalising results in Southeast Asia and beyond

We believe the results presented here are typical of conditions in many similar forests in the region that are fragmented or adjacent to oil palm (e.g., southern Thailand, and throughout Malaysia and Indonesia). High wild boar densities have been reported in fragmented forests and in forest edges throughout Southeast Asia, especially where their predators have been extirpated or where their food supply is subsidised by neighbouring agriculture (Love et al., 2018; Luskin et al., 2014, 2017). Other forests in Southeast Asia are also heavily defaunated, or at least hunting pressure is so intense that even wild boar densities are suppressed below historical levels

(Harrison et al., 2016). For example, evidence from a hunted forest in Malaysian Borneo suggests that the decline in herbivore populations, including the bearded pig (*Sus barbatus*), was associated with a dramatic increase in tree sapling densities (Harrison et al., 2013). However, shifts in liana abundance were not reported in that study or in other studies from the region. Defaunation effects on forest community composition depend on how specific animal guilds are impacted (Dirzo et al., 2014; Harrison et al., 2016).

4.4 | Impacts on forest function differ from Neotropics

Previous work in the Neotropics has suggested that hunting of wildlife that disperse seeds can reduce forest carbon storage via a decline in the regeneration of larger-statured and higher wood density tree species that are primarily vertebrate-dispersed (Osuri et al., 2016). This is thought to be a consequence of the different reproductive ecologies of trees and lianas in Neotropical rain forests. Over 75% of Neotropical trees produce fruits dispersed primarily by vertebrates making these species highly susceptible to the effects of hunting of seed dispersers (Gentry, 1982; Muller-Landau & Hardesty, 2005; Peres & Van Roosmalen, 2002). On the contrary, about 60% of Neotropical liana species are wind-dispersed and thus less dependent on wildlife for their reproduction. In Pasoh, where 81% of tree species and 70% of liana species are vertebrate dispersed (Wright et al., 2015), the impact of wildlife appears to be quite different from the Neotropics. Assuming that dispersal is a requirement for successful recruitment, Old World lianas will not indirectly benefit from the loss of seed dispersers to the same extent as in Neotropical lianas. Empirical evidence and modelling both suggest that carbon losses in hunted forests may occur in the Neotropics but not in Southeast Asia (Harrison et al., 2013; Osuri et al., 2016; Schnitzer, 2015). The differences between Pasoh and Neotropical forests may also be explained by differences in the dominant wildlife species and their specific behavioural characteristics. In Pasoh, wild boars are both seed and sapling predators having a major impact on regeneration, whereas peccaries and other native large Neotropical vertebrates may not build nests, leading to comparatively smaller their effects on tree and liana regeneration (although see next section on invasive wild boars).

4.5 | Cascading impacts from wild boar outside Asia

Similar indirect long-term impacts from wild boar likely extend outside Southeast Asia, especially where wild boars are invasive. Wild boars have invaded a variety of forested and non-forested temperate and tropical ecosystems, including both degraded and undisturbed sites (Barrios-Garcia & Ballari, 2012). Their success is attributed to their high reproductive rates and wide niche breath, both in terms of their generalists omnivorous diet, phenotypic and behavioural plasticity to survive in a variety of climates, and few specific habitat requirements (Sales et al., 2017). There is already significant literature on the ecological and economic impacts of invasive wild boars and

longer-term nuanced datasets will increasingly enable ecologists to continue tracking the cascading impacts and changes to plant functional traits (Barrios-Garcia & Ballari, 2012). This has become a research focus in the Neotropics and especially Brazil where wild boar have already become an important component of many ecosystems (Pedrosa et al., 2015; M. Pires & M. Galleti, in prep). Wild boar interactions with native mammals and humans are also be important in shaping their direct and indirect effects on plants. In Brazil, for example, in the absence of hunting, wild boars may displace native species like peccaries but not replace their ecological function, but where hunting is common, hunters may focus on wild boar thus shielding native mammals (Pedrosa et al., 2015).

4.6 | Management implications

Our results have clear management implications: forest edges and fragments are prone to cryptic long-term cascading effects that should considered in conservation planning. First, edges and fragments routinely suffer altered wildlife abundances due to hunting, predator losses (trophic cascades), or availability of nearby food (cross boundary subsidy cascades). Second, modified wildlife communities produce secondary cascading impacts on the vegetation, even shifting the plant functional types that are crucial to forest structure and function, as we showed for trees and lianas in this study. Effective management of crop-raiding species may limit cascades, especially for non-threatened species such as wild boars or macaques. The most relevant approach would be culling or regulated hunting (Luskin et al., 2014). However, encouraging hunting in areas where there are also many endangered species is risky and requires effective monitoring and enforcement.

4.7 | Future work

The precise contribution of wild boar versus other wildlife species in shifting seedling dynamics remains unclear. Further work with camera traps to assess the source of stem damage will help resolve the specific role of different animal species and importance of different plant–animal interactions, such as herbivory versus trampling and seed predation versus seed dispersal. These questions might also be addressed by experimentally excluding specific of guilds of animals. Replicating our study across a diversity of tropical forest fragments would be useful in exploring how different types of landscape configurations and perturbations affect ecological cascades. An important question we did not assess is how plant compositional changes impact larger scale ecosystem processes like carbon storage, such as was simulated for Neotropical forests by Peres et al. (2016). Finally, research on management techniques to control wild boars are in dire need in the region and globally.

5 | CONCLUSIONS

A prominent conservation issue for modern tropical forests is altered faunal communities that trigger cascading impacts on plant

communities. Three common faunal outcomes in disturbed or fragmented forests are (a) declining wildlife populations due to hunting, (b) trophic cascades following the loss of predators, which leads to increased herbivores, omnivores and/or mesopredators, and (c) food subsidies from nearby farmland, leading to selective increases in crop-raiding generalist species such as wild boars (a 'cross boundary subsidy cascade'). Our study indicates that these distinctive faunal outcomes trigger unique cascading impacts on plant communities by differentially shifting the regeneration of trees and lianas. As these two plant functional types dictate important aspects of forest structure and function, we caution that altered wildlife communities may have important long-term impacts on forest ecology and ecosystems services that are yet to be fully appreciated.

AUTHORS' CONTRIBUTIONS

M.S.L. and K.I. conducted the fieldwork, M.S.L. analysed the data, M.S.L. and S.J.D. wrote the paper, and all authors contributed to the final version of the manuscript.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/doi:10.5061/dryad.91ht938 (Luskin, Ickes, Yao, & Davies, 2019).

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