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Sapling data is available through the ForestGEO web portal:

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#Title

Wildlife disturbances as a source of conspecific negative density dependent mortality in tropical trees

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#ABSTRACT

Large vertebrates are rarely considered important drivers of conspecific negative density-dependent mortality (CNDD) in plants because they are generalist consumers. However, disturbances like trampling also cause plant mortality, and their impact on plant diversity depends on the spatial overlap between wildlife habitat preferences and plant species composition. We studied the impact of native wildlife on a hyperdiverse tree community in Malaysia where pigs (*Sus scrofa*) are abnormally abundant due to food subsidies in nearby farmland. Pigs construct birthing nests using hundreds of tree saplings, which accounted for at least 18% of tree sapling mortality at our site. We tagged 34,950 tree saplings in 25-ha plot during an initial census and assessed the likelihood they were later killed by pig nesting disturbances in subsequent years (N = 1,672 pig-induced deaths). At the stand scale, pigs nested in flat dry habitats, and at the local neighborhood scale, they nested within clumps of saplings, both of which are intuitive for safe and efficient building. At the stand scale, flat dry habitats contained higher sapling densities and higher proportions of common species, so pig nesting increased the weighted average species evenness across habitats. At the neighbourhood scale, pig-induced sapling mortality was associated with higher heterospecific and especially conspecific sapling densities. Tree species have clumped distributions due to dispersal limitation and habitat filtering, so pig disturbances in sapling clumps indirectly caused CNDD. As a result, Pielou species evenness in 400-m² quadrats increased 105% more in areas with pig-induced deaths than areas without disturbances. Wildlife induced CNDD and this supported tree species evenness but they also drove a 62% decline in sapling densities, which is unsustainable. We suspect pig nesting is an important feature shaping tree composition throughout the region.

INTRODUCTION

Plant community dynamics are shaped by plant-animal interactions such as seed dispersal, seed predation, herbivory, and trampling [1–3]. The potential for large (>10 kg) wildlife to increase tropical tree diversity has

been demonstrated by the positive effects of seed dispersal [1,4]. However, the effect of large wildlife consuming or trampling plants on tree diversity has rarely been considered because large animals are rarely species-selective [5–9]. Non-selective wildlife disturbances can still support tree diversity if the spatial patterns of habitat use disproportionately affect common species and help limit local or community dominance [10].

Local plant diversity is maintained through a variety of mechanisms, such as niche differentiation, and conspecific negative density-dependence (CNDD). CNDD occurs when a species' mortality rate increases with its density, and this supports diversity and coexistence by limiting local dominance [11]. CNDD can either arise from stronger intraspecific competition than interspecific competition, or higher attack rates by plant enemies for common and/or clumped species [8,11]. For example, the Janzen-Connell Hypothesis posits that there are higher attack rates by specialist natural enemies (mostly host-specific arthropods and fungi) in offspring clumps nearby parents, thereby inducing CNDD [8]. Small mammals have non-selective diets have only occasionally been found to induce CNDD, and only at the seed stage [12,13]. Larger herbivorous and omnivorous vertebrates >1kg (hereafter 'wildlife') with broader generalist diets and higher mobility have not been considered important sources of CNDD for seeds, seedlings, or saplings [6,8].

In addition to consumptive effects from herbivory, wildlife also physically disturb plants, but how this influences plant diversity has rarely been assessed. In tropical forests, a study monitoring artificial seedlings found that 59-77% were severely damaged in unhunted forests over a 12-mo period, which was 350% higher than in hunted forests, and suggests that trampling is an important source of damage for tree seedlings and saplings [14]. Non-random patterns in wildlife habitat use at the local scale and across a landscape can result from behaviors such as the avoidance of steep slopes or areas with high predation risk ('landscapes of fear') [9,15]. Wildlife may also avoid areas with denser tree saplings for ease of navigation, or alternatively, wildlife may prefer dense patches of saplings for cover from predators or for nesting opportunities. This effects of wildlife selective habitat-use on plant species depends on the underlying plant community composition. To better understand the role wildlife may play in shaping tree composition, we examined if the spatial patterns of wildlife disturbances (i) overlapped with common tree species distributions, (ii) if wildlife targeted heterospecific or conspecific sapling aggregations, and (iii) if areas with wildlife disturbances experienced different trends in species richness and species evenness.

Tropical forest tree species saplings tend to be spatially aggregated at the stand-scale (i.e. 25 ha; [16] due to abiotic habitat filtering [17–19] and at the local neighbourhood-scale due to dispersal limitation (i.e. 0.04 ha). Thus, wildlife disturbances in specific habitats could affect a subset of species and disturbances in sapling clumps may disproportionately kill locally abundant species (figure 1). If common species are more likely to die from wildlife than rare species due to their habitat preferences, this would increase species evenness of the stand-scale, but may not affect coexistence. Within a habitat, if a species likelihood of dying from wildlife disturbances increases with their local density, then wildlife disturbances would induce CNDD at the local neighbourhood scale, and this may contribute to species evenness and coexistence [20].

Our study focuses on disturbances from native wild boars (*Sus scrofa*, hereafter ‘pigs’) in a primary tropical rainforest called the Pasoh Research Forest in central Peninsular Malaysia. Pasoh is a large forest reserve with continuous connectivity to other forests and possesses a thriving wildlife community [21,22]. Southeast Asian native pigs often subsidized their omnivorous diet by crop raiding on fruits in oil palm plantations, leading to much higher densities than in interior forest areas [21,23–25]. Pigs can suppress tree regeneration through seed predation, rooting, and seedling trampling [21,26] but have minor consumptive effects on larger saplings because they are not browsers (nor are they seed dispersers [27]). In Peninsular Malaysia, pigs’ most important impacts on tree saplings come from their nests, which pregnant pigs build to provide cover during birth and the first days of nursing. A single pig nest can include hundreds of tree saplings collected from a small area (ca. 0.025 ha) [28]. At Pasoh, nest building by crop-raiding pigs was identified as the main driver of a 62% decline in tree sapling densities from 1986-2010 [21], but it remains unclear how pig nesting affects tree diversity.

We examined the patterns of tree sapling mortality due to pig nesting and linked this to changes in tree diversity over a 5-yr period. We were able to identify pig-induced mortality by directly retrieving previously tagged saplings from pigs nests. We tested if the spatial patterns of pig nest-induced mortality differed from other sources of mortality using individual-based mortality models. We tested if pig nesting was associated with specific habitats and tested for CNDD by including sapling neighbourhood heterospecific and conspecific densities as covariates in the mortality models. We used three models (different response variables) to compare patterns of mortality from pigs, mortality from other sources, and if pig-induced mortality patterns differed from other sources. In separate models, we tested if pig nesting induced higher species richness and evenness by comparing diversity changes in areas with and without pig nesting damage. This approach allowed us to test three hypotheses about how the spatial distribution of pig disturbances could alter sapling diversity (detailed in table S1 and illustrated in Figure 1):

- (1) Pigs nest in abiotically-defined habitats (dry flat areas). If these preferred nesting areas overlap with habitat associations of more common sapling species, then the per capita pig-induced death rate may be higher for common species, supporting species evenness of the stand (>10 ha).
- (2) At the local neighbourhood scale (<1 ha), pigs choose nesting sites where there are many saplings (clumps) to efficiently construct their nests. Saplings with higher neighborhood densities (stems from all heterospecifics) will face higher mortality from pigs, thereby reducing the spatial variation in stem densities but not causing CNDD or increasing species evenness.
- (3) Since species tend to be spatially aggregated due to abiotic habitat filtering and dispersal limitation, if pigs target any sapling clumps for nesting materials, then saplings with higher conspecific neighborhood densities may face higher risk of mortality from pigs. This will cause ‘pig induced CNDD’ and increase neighbourhood-scale species evenness.

METHODS

Study site

Our study was conducted at the 1813-ha Pasoh Research Forest located within the 12,507-ha Pasoh Forest Reserve in Negri Sembilan, Malaysia (hereafter Pasoh; 2°58'47"N, 102°18'29"E). The primary lowland forest has a 40–60 m tall canopy dominated by trees in the Dipterocarpaceae [29]. Our study made use of the 50-ha forest dynamics plot (FDP) established in 1985 [30]. The plot is in the center of the reserve, >1.35 km from any edge. Elevation within the 50-ha plot ranges from 80–110 m above sea level. The plot includes four distinct edaphic habitats: hills had well-drained shale-derived soils and laterite-derived soils, and low-lying and flatter areas 'dry alluvial soils' and 'wet alluvial soils' [30].

Pasoh has a diverse wildlife community, including several species of primates, deer, mousedeer, hornbills, civets, as well as tapirs (*Tapirus indicus*), sun bear (*Helarctos malayanus*) and a number of predatory cat species including leopards (*Panthera pardus*) [21]. The seed-dispersing community has not appreciably changed from 1986 to present [21]. However, there is an over-abundance of native pigs (*Sus scrofa*), whose densities were estimated from distance sampling at 27–47 individuals per km² during the study period (Ickes 2001).

Tree sapling censuses

All tree stems ≥ 1 cm dbh were identified, mapped, and measured in a 25-ha area in 1995 and 2000 [29]. In calculating the neighbourhood statistics for all saplings, we had to exclude the borders of the plot and this left a 22.08-ha study area where all stems could be associated with all habitat and neighbourhood variables. We focused on 34,950 stems in the 1.0–1.5 cm dbh size class, hereafter called saplings, because pigs primarily use this size class and smaller for their nests [21,28]. We categorized 1995 saplings into three groups: (1) 'survivors': saplings with dbh ≥ 1 cm in the 1995 and 2000 censuses, (2) 'pig-induced mortality': saplings with dbh ≥ 1 cm in the 1995 whose stem tags were found in pig nests, and (3) 'other-deaths': saplings in the 1995 that were marked 'dead' or 'missing' in the 2000 census but not found in pig nests.

Pig nest surveys

We identified pig-induced mortality by excavating the tree tags from the forest dynamics plot (FDP) found within pig nests in a 25-ha study area in 1996 and 1998 (figure 1) [28]. At Pasoh, each pig nest contains an average of 267 (SD: 86) woody saplings with most smaller saplings being uprooted and larger saplings being snapped [28]. The tags linked saplings to the FDP dataset provided information on the identities, sizes, and original locations, enabling us to assess how a sapling's abiotic and biotic characteristics in the initial census affected their likelihood of being later used for nest building. Stems whose tags were found in nests were assumed to suffer 'pig-induced mortality.' As nests were only excavated in two of the five years between censuses, the other deaths include some stems used for pig nesting in unsampled years (table S4). Stems that were found in nests but did not have tags were not included in the study since their species identity or original location could not be verified.

We were interested in the spatial patterns of pig-induced sapling mortality more than the actual nesting sites themselves, but saplings are only taken from an area of 244 m², with most stems coming from within a 5 m radius around the nest site (Ickes et al. 2005). We considered that stems found in nests were killed, and although many stumps created by pigs resprout these face much higher mortality than unbroken stems [28,31].

Tree sapling mortality analyses

We used individual-based Generalized Linear Mixed Models (GLMMs) to assess the likelihood of saplings being found in pig nests (pig-induced deaths) and likelihood of dying due to other causes. In the GLMMs, there was a binary response variable (0,1) where 0 corresponded to survival and 1 for death, and we used binomial-family error distributions. We included explanatory variables (covariates) to evaluate which factors influenced the odds of mortality where all continuous variables were centered on the mean and standardized by one standard deviation. Each parameter estimated by the GLMM (on the logit scale) represents the change in log odds that a sapling died in the study period with a one standard deviation increase in the corresponding variable.

We constructed three GLMMs to test the influence of the covariates on the odds of mortality: (GLMM1) pig-induced deaths versus survivors, wherein we set the binary response to one for pig-induced deaths and zero for survivors (hypotheses 1-3), (GLMM2) other-deaths versus survivors, wherein we set the binary response one for other-deaths and zero for survivors (hypothesis 4), and (GLMM3) pig-induced deaths versus other-death saplings, wherein we set the binary response to one for pig-induced deaths and zero other-deaths. This last model assessed if the effects from pigs significantly differed from background mortality.

Our three hypotheses are tested in each model by assessing the significance of three key covariates. Firstly, to test the hypothesis that pig mortality varied between habitats, we included the abiotic habitat type where each tagged sapling found in a nest was located in all models. Secondly, to assess if pigs caused higher mortality in clumps, we included the heterospecific density around each sapling in all models. Thirdly, to assess if pigs caused conspecific negative density dependence (CNDD), we included the conspecific density around each sapling in all models.

In all GLMMs, we accounted for spatial autocorrelation among nearby stems by including a random intercept for each 10 X 10-m subplot ($N = 2196$) to allow for shared responses within localized areas (Johnson et al. 2017; McFadden et al. 2019). We assessed if there was support for interactions using model selection by comparing Akaike information criterion (AIC) values. There was no support for interactions among variables in the models presented in this study. To assess significance of predictors included in the GLMMs, we used Satterthwaite approximations for the degrees of freedom and report z-values and P-values (lmerTest package in R [34]). Degrees of freedom are not provided in the lme4 package for GLMMs for conceptual reasons, although it should be noted that our sample sizes were very large (34950 stems) and we limited our predictors to <10 variables that included <20 total factor levels.

Predictors of sapling mortality

In each GLMM, we tested for whether pigs targeted sapling clumps by including the heterospecific sapling abundance within 5-m radius neighbourhoods (calculated for each sapling) and we tested for CNDD by including the conspecific sapling abundance in the 5-m radius neighbourhood. We tested if common species faced higher mortality by including the species stand-level abundance (total saplings of each species in the 25-ha study area).

In each GLMM, we assessed if local abiotic factors (elevation, slope, and soil habitat type) were associated with the odds of mortality (table 1; figure 1). For the soil type variable (descriptions in Study Site section), dry alluvial soil was included as a categorical variable and compared to the other three soil types combined (grouped), because the other three soil types showed no difference in their effects on mortality. All models included the sapling dbh as a predictor of mortality because previous work has shown pigs prefer smaller saplings [21]. To address whether certain life history strategies were more prone to pig induced mortality, we included whether the species was pioneer versus a seral or late-successional species, as identified by Davies et al. (2003), as since these species are known to have higher recruitment and mortality rates. We used AIC model selection to confirm reducing the levels of this categorical variable improved model fit.

Tree diversity in quadrats with and without pig nesting

We assessed changes in sapling density and diversity between 1995 and 2000 within 400 m² quadrats (20 x 20 m; hereafter ‘quadrats’) using linear regressions (LR). The LR response variables were differences in sapling density, species richness or species evenness between the censuses, measured for each 400 m² quadrat (N = 554). We included a dummy variable (0 or 1) to assess if changes in density and diversity differed between quadrats with ≥1 pig-induced sapling deaths versus those with zero pig-induced sapling deaths. The evenness values were calculated as the Pielou index (J’), which is derived from the Shannon index and ranges from 0.0 to 1.0, with higher values representing more even species distributions [35]. A key aspect of Pielou evenness is that it represents the relative evenness, which is the proportion of maximum possible evenness given a particular number of species within the sample, and is unbiased to differences in sample sizes and species richness [36].

Determining if rare species were spared from pig nests

We assessed if the composition of saplings in pig nests was representative of the community using the Wilcoxon rank sum test comparing the species abundance distributions among species found within nests differed the those for species that were never found in nests. We evaluated if the actual species richness found within nest saplings differed from a random sample of the entire 1995 baseline community using the Kolmogorov-Smirnov test. For the latter, we created a null distribution of expected species richness among nest saplings – assuming pigs harvested randomly - by simulating 10000 random subsets of 1,672 stems (number of stems recovered from pig nests) taken from the full community of 34,950 saplings. All statistical analyses were conducted using the statistical program r version 3.5.1.

RESULTS

Tree sapling mortality

There were 34,950 saplings (1.0-1.5 cm dbh) alive in 1995 from 661 species in the 22.08-ha study area. In the 2000 census, 8,911 (25.5%) had died or were broken below measurement height (assumed to have died), of which 1,672 (18.76%) were found in pig nests (‘pig-induced deaths’) in the 1996 and 1998 surveys and 7239 (81.2%) were not associated with pig nests in these two years (‘other-deaths’).

Pigs nesting removed 6.24% of stems from dry alluvial soil habitats and 2-3% of stems in each other habitat. There were higher sapling densities in lower elevations, flatter areas, and in dry alluvial soils (table 1, figure 1 & S2). Dry alluvial soils also contained more common species than the other habitat types, as measured by the average stand-wide abundance of stems found in each soil type. Pielou species evenness was also 6.9-8.7% lower in alluvial habitats than the other three soil types (LM: $df = 34948$, $t = -109.4$, $P < 0.001$). Species stand-wide abundance was positively correlated with both conspecific and heterospecific densities, meaning that common species are more likely to be found in denser areas of saplings (table 1 & figure S2).

Pig-induced mortality patterns differed from other sources of mortality

Within the 1.0-1.5 dbh size class of saplings, those with smaller dbh were significantly more likely to suffer pig-induced deaths (GLMM coefficient: z -value = -20.234, $P < 0.001$ in GLMM 1) and other-deaths ($z = -17.744$, $P < 0.001$ in GLMM 2; figure 2; table S5). Sapling pig-induced deaths showed clear abiotic associations revealed by positive relationships with topographic position (slope), elevation, and dry alluvial soil habitats ($z < -5$ and $P < 0.001$ for all three), and all three abiotic variables were stronger predictors (larger parameter magnitude) of pig-induced deaths than other deaths ($z > 4$ and $P < 0.001$ for all three). The effect of being a pioneer species was not a significant predictor of pig-induced deaths ($z = 1.840$, $P = 0.066$) but pioneers did have greater odds of other-deaths ($z = 3.148$, $P = 0.002$).

The GLMM 1 results (pig-induced deaths versus survivors) revealed that higher neighbourhood conspecific densities increased the odds of pig-induced mortality ($z = 4.760$, $P < 0.001$). When including abiotic habitat variables, which were correlated with heterospecific neighbourhood densities (figure S2), then there was no significant effect of heterospecific density on the odds of pig-induced mortality ($z = 1.165$, $P = 0.244$; table S5). A reduced version of GLMM1 that omitted abiotic variables revealed that neighbourhood heterospecific density increased the odds of pig-induced mortality ($z = 2.899$, $P = 0.034$; figure s3; table S6). Likewise, a reduced version of GLMM1 including only stem diameter and species abundance as fixed effects indicated that species with higher stand-level abundance faced higher odds of pig-induced mortality ($z = 3.911$, $P = 0.019$). The significance of these parameters in reduced models but not full models is explained by conflation of habitat variables (elevation, slope, and soils) with neighbourhood heterospecific density and species stand-level abundance (figure 2).

Other work as suggested that CNDD may vary with species abundance [20]. We tested this by including an interaction term between neighbourhood conspecific density and species stand-level abundance GLMM1. We found no support that CNDD from pigs varied with species stand-level abundance when controlling habitat covariates ($z = 0.098$, $P = 0.922$) or excluding habitat covariates ($z = 0.398$, $P = 0.690$).

The GLMM 2 results (other-deaths versus survivors) also revealed that neighbourhood conspecific density increased the odds of pig-induced mortality ($z = 3.051$, $P = 0.002$), albeit this effect size was significantly smaller than for pig-induced deaths ($z = 2.886$, $P < 0.001$). However, increasing heterospecific neighbourhood densities reduced odds of mortality ($z = -7.967$, $P < 0.001$), indicating dense neighbourhoods had higher odds of

survival, and which was the opposite direction as its effect on pig-induced mortality (figure 2; table S5). Stand-level species abundance was negatively associated with odds of other-deaths ($z = 3.068$, $P = 0.002$), suggesting common species suffer lower odds of mortality, again the opposite effect as for pig-induced mortality. Most covariate estimates significantly differed between pig-induced deaths and other deaths ($P < 0.02$ for all comparisons in table S5 & S6), showing pigs produced distinct patterns of sapling mortality.

Diversity in quadrats with and without pig nesting

Of the 554 quadrats in the sample area, Pielou evenness increased in most quadrats, but increased 105% more in the 291 quadrats with pig-induced deaths than without pig-induced deaths (LR: $df = 1101$, $t = 4.02$, $t = -13.977$, $P < 0.001$; table S7). In the initial census, quadrats that latter suffered pig-induced deaths were 19.8% more dense (LR: $df = 1104$, $t = -12.06$, $P < 0.001$), had 9.1% higher species richness (LR: $df = 1104$, $t = -11.27$, $P = 0.001$) and had 1.5% lower Pielou evenness (LR: $df = 1104$, $t = 4.25$, $P < 0.001$) than quadrats without pig-induced deaths (figure 3; table S7). Between the two censuses, the sapling densities declined 38.1% more in quadrats with pig-induced deaths (LR: $df = 1101$, $t = -5.435$, $P < 0.001$). Among the quadrats with pig-induced deaths, sapling species richness only declined 2.72% despite a 27.8% decline in mean sapling abundance during the study period.

Rare species were spared from pig nests

Of the 661 species of saplings in 1995, only 322 species were found in nests, statistically fewer than expected by chance (figure 3e). The species stand-level abundance distributions differed between nest-species and those species never used in nests (Wilcoxon rank sum test, $P = 0.002$; figure 3f), with more abundant species suffering higher pig-induced death rates (Kolmogorov–Smirnov test, $d = 0.114$, $P < 0.001$; figure 6c). The average stand-level sapling abundance for species suffering pig-induced deaths was 452.3 stems, 17.8% higher than the average abundance of a surviving stem (384 stems), and 16.4% higher than other-dead saplings (388.5 stems; LR: $df = 34948$, $t = 10.197$, $P < 0.001$).

DISCUSSION

Our study illustrates that wildlife can alter tropical tree diversity through stand-scale and neighborhood-scale habitat preferences. Specifically, at the stand scale, we found native wild pigs’ nest building habitat selection for unflooded alluvial soil habitats overlapped with the habitat associations of common tree species at our site. This increased the weighted average species evenness across habitats. Rarer species from smaller habitats may not replace those common stems killed by pigs due to habitat filtering, so this mechanism may not support coexistence. At the neighborhood-scale (e.g. within a single habitat), pig-induced mortality was associated with conspecific density thereby inducing CNDD, which increased species evenness. This enemy-driven cause of CNDD may support a coexistence, much in the same way that Janzen-Connell effects cause CNDD and support coexistence.

Pigs’ habitat preferences for nest building were logical for safe and efficient construction, and thus supported our hypotheses 1-3. First, pigs preferred flat dry habitats, which would intuitively reduce the likelihood of nests

flooding or toppling. Second, pig-induced sapling mortality was also associated with local sapling densities, which would be suitable for optimal forging of nest materials. Tree sapling of the same species are often aggregated due to dispersal limitation and fine-scale habitat filtering [16–19,37], and we predicted and found that stems with nearby conspecifics were more likely to suffer pig disturbances. This indirectly caused CNDD.

These results are ecologically significant because pig nesting was responsible for at least 18% of sapling mortality at our site, and quadrats with nest mortality showed 105% greater increases in species evenness than quadrats without nest mortality. Pielou's evenness increased by 0.49% in 20-m neighborhoods around pig-induced death-saplings over just five years, which is equivalent to 9.8% per century. Pigs also had a small negative effect on species richness, which slightly declined by 2.72% due to sampling effects (fewer total stems). While our study focused on the processes explaining shifts in diversity from 2000-2005, another study from site found sapling species evenness increased consistently between 1986-2010 [21], suggesting pigs' impacts on diversity are a persistent feature of this forest.

Pig as tree enemies

Since pigs kill saplings, they can be considered as enemies within the framework of the Janzen-Connell Hypothesis (JCH). However, most realizations of JCH ascribe CNDD in saplings clumps nearby parents to growing populations of dispersal-limited and host-specific arthropods and fungi enemies [8]. Our focal enemies (pigs) is a generalist mobile omnivore and their populations do not increase in conjunction with a particular host tree species. Therefore, our case represents a new variety of enemy-mediated CNDD within the broader JCH framework, and provides a robust and intuitive example of how wildlife can induce CNDD that is missing in the literature.

Positive density dependence among non-pig afflicted saplings

Pig-induced sapling mortality showed opposing patterns compared to mortality from other sources. This illustrates wildlife can inflict fundamentally different processes, and not just reinforce other mortality processes. For example, both pig-induced mortality and other-sources of mortality showed significant CNDD, so in this case pigs would reinforce CNDD processes that might have arisen due to enemy-mediated JCH effects or intra-specific competition [32,38]. However, while pig-induced mortality was positively associated with heterospecifics densities, other sources of mortality showed lower mortality in clumps, indicating heterospecific *positive* density dependence [39].

Results presented are conservative

Our results likely underestimate the effect of pig-induced increases on tree sapling evenness for three reasons. Firstly, most stems used in nests are <1 cm dbh so, by focusing on larger saplings, we only captured a fraction of the total pig-induced mortality [21]. Secondly, a considerable number of tags from pig-induced death-saplings were not found in the pig nests, as some would have fallen off when the stem was snapped and carried to nests. This was apparent because the number of saplings >1 cm found in nests was much higher than the actual number of tags recovered, meaning we underestimated all pig-induced deaths. Thirdly, nest surveys were

not available for 1997, 1999 and 2000 and consequently, saplings labeled ‘other-deaths’ likely include many pig-induced deaths from these years yielding another source of underestimation.

Longer-term implications for tree recruitment

However, we do not suggest that pig nesting disturbances observed at Pasoh are necessarily representative of other sites, or that the observed impacts at Pasoh will have lasting effects on diversity, because pig densities are elevated at our site and wildly fluctuate between decades [21]. We narrowly focused on trees in this study, but pig disturbances at Pasoh has also been shown to increase the relative abundance of lianas [40], which suppress tree survival and growth [41], and contributes to spreading invasive species [42]. Finally, tree species with more aggregated distributions may be a higher risk of pig nesting damage, such as ballistic and wind-dispersed species that are more aggregated than vertebrate-dispersed species [17].

Conservation implications

The findings presented here show that elevated pig populations can affect forest diversity over a relatively short time, which may have regional and global conservation repercussions. Defaunated forests may be missing these key wildlife disturbances that contribute to the maintenance of hyperdiverse plant communities. While severe ongoing pig-inflicted mortality would eventually reduce richness and cause negative cascading impacts on forest.

Our previous work from the site has shown that oil palm provides food subsidies to crop-raiding pigs and this triggers ecological cascades affecting tree densities that reach >1km into the interior of protected areas [21]. This study extends this work in showing that subsidy cascades can also influence CNDD and tree diversity. Currently, there are ~7 Mha of oil palm and ~15 Mha of forest in Malaysia, with most forests being fragmented and close to oil palm plantations [43,44]. Pigs are now over-abundant in many forests in Southeast Asia [23–26] and pigs are invasive in other oil palm growing regions [27]. Mitigating the impacts from pigs on forests could be accomplished through fencing farmland or managing pigs, such as through culling or controlled hunting.

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AUTHORS’ CONTRIBUTIONS

M.S.L. designed the study and analysed the data. K.I. conducted the pig nest surveys, Y.T.L. and S.J.D. manage the tree census database, and D.J.J. assisted with the data analysis. M.S.L., S.J.D. and D.J.J. wrote the paper. All authors contributed to the final version.

DATA ACCESSIBILITY

Nesting data is available via the Dryad Digital Repository [https:// dryad.XXXX](https://dryad.XXXX) (Luskin, Ickes, Yao, & Davies, 2019) and tree census data is available at <https://forestgeo.si.edu/sites/asia/pasoh>.

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Soil habitat	Total stems in habitat	Stems found in pig nests	% stems found in pig nests	Elevation (mean)	Slope (mean)	Stand-wide species abundance (median)	Species richness	Pielou species evenness
Wet alluvial	8034	237	2.950	81.65	1.15	124	533	0.849
Dry alluvial	20207	1261	6.240	82.88	0.95	234	575	0.791
Laterite-derived	4288	120	2.799	89.80	5.14	139	439	0.866
Shale-derived	2421	54	2.230	90.84	4.25	118	362	0.877
Totals	34950	1672	4.784					

Table 1 Characteristics of sapling communities in each of the four main soil habitats. Stand-wide species abundance is the total number of saplings 1-1.5 cm dbh in the 25 ha plot for each species, and the table shows the median value among stems located in each habitat.

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Figure 1 Locations of pig nests, hypotheses about pig nesting habitat preferences, and habitat characteristics of sapling that were found in nests. (a) Locations of pig nests (black points) in the 25 ha study area, colored by soil habitat type, with legend matching colors in panels d and e). In the inset, local sapling neighborhoods are shown with tree species represented by different colors. Hypotheses are described in the text and table S1. (b) The 33,278 sapling stems that were not used in pig nests, plotted in elevation-slope habitat niche-space and colored by soil types (matching colors in panels d and e). Wet and dry alluvial soils are flat low-lying areas, laterite-derived and shale-derived soils are found on hills. (c) The 1,672 stems that were later recovered in pig nests, showing a clustering in low elevation, low slope sites with dry alluvial soils (orange color). (d) Mean sapling density in different in soil habitats. Letters indicate significant differences at the $P < 0.05$ level assessed using LMMs. (e) Average species stand-wide abundance for stems found in different soil habitats, showing dry alluvial soils contain more common species.

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516 **Figure 2** Predictors of sapling mortality due to pigs (orange) versus other sources, assessed with an individual-
517 based mortality model (GLMMs). Odds ratios above 1 indicate increased mortality among the 34,950 saplings.
518 There were 1,672 stems found in pig nests in 1996 or 1998 and 7,285 stems that died for other reasons. Values
519 are the GLMM coefficient estimates and errorbars show 95% CI. Closed circles show results with $P < 0.05$ and
520 open circles show results with $P > 0.05$. All continuous variables were scaled (mean of 0 and sd of 1).
521 Heterospecific and conspecific densities are measured within 5-m radius neighbourhoods of every stem. As an
522 example of how to interpret the terms, the negative stem diameter coefficients indicate that larger stems had
523 lower chance of dying, and this relationship was significantly stronger for pig-induced deaths than other-deaths.
524 Full model output is presented in table S4.

Figure 3 Impacts on pig nesting on tree sapling compositions and diversity. Sapling density (a), species richness (b), and Pielou species evenness (c) in 400 m² quadrats in 1995 and 2000, separated by those quadrats with at least one pig-induced death-sapling (N = 293; orange) versus quadrats with no known pig-induced deaths (N = 261; green). Letters indicate significant differences at the P < 0.05 level. (d) Species abundance distributions of the 339 species found in nests (green histogram) versus the 332 that were never found in nests (orange histogram; Kolmogorov–Smirnov test, $d = 0.114$, $P < 0.001$). The histogram area for each group is equal to one. (e) The predicted number of species that would be found in pig nests in our study (grey histogram) versus the actual number (322 species, orange; Wilcoxon rank sum test, $P = 0.002$). The grey histogram is the null expectation produced by random drawing 1,672 stems (actual tags recovered from nests) from the 34,950 possible stems available in the in the 20.08 ha study area. (f) Changes in Pielou's species evenness, measured in square subplots. We used LMM to test if the change in diversity differed from zero and all four subplot sizes showed highly significant differences ($P < 0.001$ for all).

Wildlife disturbances as a source of conspecific negative density dependent mortality in tropical trees

ABSTRACT

Large vertebrates are rarely considered important drivers of conspecific negative density-dependent mortality (CNDD) in plants because they are generalist consumers. However, ~~non-consumptive~~ disturbances like trampling also cause plant mortality, and their impact on plant diversity depends on the spatial overlap ~~of~~ between wildlife habitat preferences and plant species composition. We studied the impact of native ~~pigs (*Sus scrofa*)-wildlife~~ on a hyperdiverse tree community in Malaysia where pigs (*Sus scrofa*). Pigs are abnormally abundant at the site and Pigs construct birthing nests using hundreds of tree saplings, which accounted for at least 18% of tree sapling mortality at our site-at our site. ~~To assess the impact of pig nesting on tree diversity,~~ We tagged 34,950 tree saplings in 25-ha plot during an initial census and assessed the likelihood they were later killed by pig nesting disturbances in subsequent years (N = 1,672 pig-induced deaths). At the stand scale, ~~p~~Pigs nested in flat dry habitats that contained higher sapling densities and higher proportions of common species at the stand scale. As a result, of the 661 species of saplings available, only 322 species were ever found in nests ~~ss, which is statistically fewer than expected by chance~~. At the neighbourhood scale, ~~p~~Pig-induced sapling mortality was associated with higher heterospecific and especially conspecific sapling densities, which is intuitive for efficient nest building at neighborhood scales. While pigs did not select specific tree species, tree species have clumped distributions due to dispersal limitation and habitat filtering, so pig disturbances in sapling clumps indirectly caused CNDD. We compared changes in sapling diversity after 5 years in 400-m² quadrats and found that Pielou species evenness in 400-m² quadrats increased 105% more in areas with pig-induced deaths than areas without disturbances. We conclude that wildlife ~~disturbances~~ can induce CNDD and ~~contribute to the maintenance of~~ support species evenness in hyperdiverse tropical rainforest tree communities. Wild pigs have become abundant in many disturbed Asian forests ~~in response to beneficial conditions because they benefit from~~ (edge habitat, food subsidies in nearby farmland, and predator declines). Thus, we suspect pig nesting is an important feature shaping tree composition throughout the region.

INTRODUCTION

Plant community dynamics are shaped by plant-animal interactions such as seed dispersal, seed predation, herbivory, and trampling [1–3]. The potential for large (>10 kg) wildlife to increase tropical tree diversity has been demonstrated by the positive effects of seed dispersal [1,4]. However, the effect of large wildlife consuming or trampling plants ~~has rarely been shown to affect on~~ tree diversity as rarely been considered because large animals are rarely species-selective [5–9]. ~~Nonetheless, it is possible for n~~Non-selective wildlife disturbances to-can still support tree diversity if the spatial patterns of habitat use disproportionately affect

common species and help limit local or community dominance [10]. To better understand the role wildlife may play in shaping tree composition, we examined if the spatial patterns of wildlife disturbances (i) overlapped with common tree species distributions, (ii) if wildlife targeted heterospecific or conspecific sapling aggregations, and (iii) if areas with wildlife disturbances experienced different trends in species richness and species evenness. altered the diversity of tree saplings in a large primary rainforest plot.

Local plant diversity is maintained through a variety of ~~Multiple~~ mechanisms, such as niche differentiation, a ~~can maintain or enhance species diversity in communities. Cnd~~ conspecific negative density-dependence (CNDD) ~~in plants. CNDD occurs when, wherein a species' mortality rates increases~~ with its intraspecific density, ~~is a mechanism to and this~~ supportss diversity by limiting local dominance [11]. CNDD can either arise from stronger intraspecific competition ~~than interspecific competition~~, or higher attack rates by plant enemies ~~for common and/or clumped species [8,11]. For example, t~~The Janzen-Connell Hypothesis suggests the attack rates of specialist natural enemies (mostly host-specific arthropods and fungi) ~~may~~ disproportionately rise with a plant species density or proximity to parents, ~~thereby inducing CNDD -[8]. Compared to insects and fungal enemies, s~~Small mammals ~~with have non-selective diets have only occasionally been found to induce CNDD within the Janzen-Connell framework, and when observed small mammal effects are and this is~~ limited to the seed stage [12,13]. ~~Meanwhile, t~~Larger herbivorous and omnivorous vertebrates ~~>1 kg~~ (hereafter 'wildlife') with broad generalist diets ~~are have not been~~ considered important sources of CNDD for seeds, seedlings, or saplings, because they are unlikely to increasingly target a single species as it becomes more common [6,8].

In addition to consumptive effects from herbivory, wildlife also ~~play an important role by~~ physically disturbing plants, but how this influences ~~tree-plant~~ diversity has rarely been assessed. ~~I-in~~ tropical forests, ~~a-A~~ study monitoring ~~fake-artificial~~ seedlings found that 59-77% were severely damaged in unhunted ~~tropical~~ forests over a 12-mo period, which was 350% higher than in hunted forests, and suggests that trampling is an important source of damage for tree seedlings and saplings [14]. Non-random patterns in wildlife habitat use at the local scale and across a landscape can result from behaviors such as the avoidance of steep slopes or areas with high predation risk ('landscapes of fear') [9,15]. Wildlife may also avoid areas with denser tree saplings for ease of navigation, or alternatively, wildlife may prefer dense patches of saplings for cover from predators or for nesting opportunities. Selective habitat-use will have distinct spatial patterning and moderate the likelihood of ~~plants suffering~~ physical damage. The consequences wildlife habitat use on ~~specific species tree-diversity~~ depends on the ~~sapling-underlying plant~~ community composition.

Tropical forest tree species saplings ~~are tend to be~~ spatially aggregated ~~at the local neighbourhood-scale due to dispersal limitation (i.e. 0.04 ha) and at the~~ stand-scale (i.e. 25 ha; [16] due to abiotic habitat filtering [17–19] ~~and at the local neighbourhood-scale due to dispersal limitation (i.e. 0.04 ha)~~. Thus, wildlife disturbances in specific habitats could affect a subset of species and disturbances in sapling clumps may disproportionately kill locally abundant species, ~~thereby inducing local neighbourhood-scale CNDD~~ (figure 1). ~~If common species are more likely to die from wildlife than rare species due to their habitat preferences, this would increase species evenness of the stand-scale, but may not affect coexistence. Within a habitat, if a species likelihood of dying from wildlife disturbances increases with their local density or clumping, thean~~ wildlife disturbances would

induce CNDD, increase species evenness at the local neighbourhood scale, and this may contribute to coexistence [20].

Our study focuses on disturbances from native wild boars (*Sus scrofa*, hereafter ‘pigs’) in a primary tropical rainforest in Peninsular Malaysia. ~~Pigs omnivorous and eat a wide variety of forest species.~~ In recent decades, Southeast Asian pigs ~~in forests nearby plantations diets are have also~~ subsidized ~~their omnivorous diet of forest resources~~ by crop raiding ~~on fruits~~ in oil palm plantations, leading to ~~much higher~~ densities ~~of >10 times higher in forests nearby plantations~~ than in interior forest areas [21–24]. In Asia, pigs can suppress tree regeneration through seed predation, rooting, and seedling trampling [23,25] but have minor consumptive effects on larger saplings because they are not browsers (nor ~~are they~~ seed dispersers [26]). In Peninsular Malaysia, pigs’ most important impacts on tree saplings come from their nests, which pregnant pigs build to provide cover during birth and the first days of nursing. A single pig nest can include hundreds of tree saplings collected from a small area (ca. 0.025 ha) [27].

We examined the patterns of tree sapling mortality due to pig nesting and linked this to changes in tree diversity over a 5-yr period. We worked at the Pasoh Research Forest in ~~central~~ Peninsular Malaysia, which is a large forest reserve with continuous connectivity to other forests and possesses a thriving wildlife community [23,28]. ~~However, Pig nesting was the main cause of there was a~~ 62% decline in tree sapling densities within the Pasoh forest dynamics plot from 1986-2010 ~~and pig nesting was identified as the main driver~~ [23], but it remains unclear how pig nesting affects tree diversity.

We were able to identify pig-induced mortality by directly retrieving previously tagged saplings from pigs nests. We tested if the spatial patterns of pig nest-induced mortality differed from other sources of mortality using individual-based mortality models. ~~We included abiotic habitat variables (elevation, slope, soils) and w~~ We tested if pig nesting ~~was associated with specific habitats or sapling aggregation patterns. We tested for CNDD induced CNDD~~ by including saplings’ neighbourhood ~~heterospecific and~~ conspecific density ~~as covariates~~ in the mortality models. ~~Finally, to determine the effect of pig nesting mortality on diversity, we compared local species richness and evenness in areas with and without pig nesting damage. We used three models (different response variables) to compare patterns of mortality from pigs, mortality from other sources, and if pig-induced mortality differed from other sources. In separate models, we tested if pig nesting induced higher species richness and evenness by comparing diversity changes in areas with and without pig nesting damage. This~~

Our approach allowed us to test four ~~specific~~ hypotheses about ~~pig nesting, which are detailed in table S1 and illustrated in Figure 1. The decline in sapling densities at the study site has already been established by previous work and attributed to pig disturbances [22], so we focus on how whether~~ the spatial distribution of pig disturbances ~~could produced alter~~ changes to sapling diversity. Our hypotheses are summarized below ~~and detailed in table S1 and illustrated in Figure 1~~:

- (1) Pigs nest in abiotically-defined habitats (dry flat areas). If these preferred nesting areas overlap with habitats ~~that contain higher relative abundances of with~~ common sapling species, then the per capita

pig-induced death rate may be higher for common species, supporting species evenness at broad scales (>1 ha).

- (2) At the local neighbourhood scales (<1 ha), pigs choose nesting sites where there are many saplings (clumps) to efficiently construct their nests. Saplings with higher neighborhood densities (stems from all heterospecific species) will face higher mortality from pigs, thereby reducing the spatial variation in stem densities but not necessarily increasing species evenness. -
- (3) Since species tend to be spatially aggregated due to abiotic habitat filtering and dispersal limitation, if pigs target any clumps for nesting materials, then At local scales (<1ha), saplings with higher conspecific neighborhood densities will face higher risk of mortality from pigs ('pig induced CNDD'). This will induce local CNDD and increases local-scale species evenness at the local neighbourhood scale (<1 ha).-
Saplings with higher conspecific neighborhood densities will face higher risk of mortality from other sources besides pigs ('other CNDD') Pig-induced mortality is random and does not cause CNDD, but other sources of mortality will show CNDD due to intra-specific competition and Janzen-Connell effects. This is a consistent finding in other studies [8,29].

(4)

METHODS

Study site

Our study was conducted at the 1813-ha Pasoh Research Forest located within the 12,507-ha Pasoh Forest Reserve in Negri Sembilan, Malaysia (hereafter Pasoh; 2°58'47"N, 102°18'29"E). The primary lowland forest has a 40–60 m tall canopy dominated by trees in the Dipterocarpaceae [30]. Pasoh is bordered on three sides by oil palm plantations that extend 4–10 km in each direction with selectively logged forest on the eastern side [31]. Our study made use of the 50-ha forest dynamics plot (FDP), established by the Forest Research Institute of Malaysia in partnership with the Smithsonian Institution's ForestGEO network in 1985 [32]. The plot is in the center of the reserve, >1.35 km from any edge. Elevation within the 50-ha plot ranges from 80–110 m above sea level. The plot includes four distinct edaphic habitats: hills had well-drained shale-derived soils and laterite-derived soils, and low-lying and flatter areas 'dry alluvial soils' and 'wet alluvial soils' [32].

Pasoh has a diverse wildlife community, including several species of primates, deer, mousedeer, hornbills, civets, as well as tapirs (*Tapirus indicus*), sun bear (*Helarctos malayanus*) and a number of predatory cats species including leopards (*Panthera pardus*) [23]. The seed-dispersing community has not appreciably changed from 1986 to present [23]. However, there is an over-abundance of native pigs (*Sus scrofa*), whose densities were estimated from distance sampling at 27–47 individuals per km² during the study period (Ickes 2001).

Tree sapling censuses

All tree stems ≥1 cm dbh were identified, mapped, and measured in a 25-ha area in 1995 and 2000 [30]. We focused on 34,950 stems in the 1.0–1.5 cm dbh size class, hereafter called saplings, because pigs primarily use

this size class and smaller for their nests [23,27]. We categorized 1995 saplings into three groups: (1) ‘survivors’: individuals with dbh ≥ 1 cm in the 1995 and 2000 censuses, (2) ‘pig-induced mortality’: individuals with dbh ≥ 1 cm in the 1995 whose stem tags were found in pig nests, and (3) ‘other-deaths’: individuals with dbh ≥ 1 cm in the 1995 and then were marked ‘dead’ or ‘missing’ in the 2000 census but not found in pig nests.

We assessed diversity changes at different scales and define ‘local diversity’ as species evenness within 400-m² quadrats (0.04 ha) and ‘large-scale diversity’ as species evenness in 1-ha quadrats. The evenness values were calculated as the Pielou index (J'), which is derived from the Shannon index and ranges from 0.0 to 1.0, with higher values representing more even species distributions [33]. A key aspect of Pielou evenness is that it represents the relative evenness, which is the proportion of maximum possible evenness given a particular number of species within the sample, and is unbiased to differences in sample sizes and species richness [34].

Pig nest surveys

We identified pig-induced mortality by excavating the tree tags from the forest dynamics plot (FDP) found within pig nests in a 25-ha study area in 1996 and 1998 (figure1) [27]. At Pasoh, each pig nest contains an average of 267 (SD: 86) woody saplings with most smaller saplings being uprooted and larger saplings being snapped [27]. The tags linked saplings to the FDP dataset provided information on the identities, sizes, and original locations, enabling us to assess how a sapling’s abiotic and biotic characteristics in the initial census affected their likelihood of being later used for nest building. Stems whose tags were found in nests were assumed to suffer ‘pig-induced mortality.’ As nests were only excavated in two of the five years between censuses, the other deaths include some stems used for pig nesting in unsampled years (table S4). [Stems that were found in nests but did not have tags were not included in the study since their species identity or original location could not be verified.](#)

This study measured pig nesting habitat preferences indirectly by noting the prior locations where the nest saplings were harvested, which provides an adequate indicator of nest location because saplings are only taken from an area of 244 m², with most stems coming from within a 5 radius around the nest site (Ickes et al. 2005). Further, we were interested in the spatial patterns of pig-induced sapling mortality more than the actual nesting sites themselves.

In calculating the neighbourhood statistics for all saplings, we had to exclude the borders of the plot and this left a 22.08-ha study area where all stems could be associated with all habitat and neighbourhood variables.

Tree sapling mortality analyses

We used individual-based Generalized Linear Mixed Models (GLMMs) to assess the likelihood of saplings being found in pig nests (pig-induced deaths) and likelihood of dying due to other causes. In the GLMMs, there was a [binomial-binary](#) response variable (0,1) where 0 corresponded to survival and 1 for death, and we used binomial-family error distributions. We included explanatory variables (covariates) to evaluate which factors influenced the odds of mortality where all continuous variables were centered on the mean and standardized by one standard deviation. [The Each parameter estimated by the GLMM \(on the logit scale\) parameter-estimates in](#)

~~the models show~~represents the change in [log](#) odds that a sapling died in the study period (~~on the logit scale~~) with a one standard deviation increase in ~~that the corresponding~~ variable.

~~ly tagged found in a nest ly~~finally

We constructed three GLMMs to test the influence of [the different variables](#)covariates on the odds of mortality: (GLMM14) pig-induced deaths versus survivors, wherein we set the binary response to one for pig-induced deaths and zero for survivors ([hypotheses 1-3](#)), (GLMM22) other-deaths versus survivors, wherein we set the binary response one for other-deaths and zero for survivors ([hypothesis 4](#)), and (GLMM23) pig-induced deaths versus other-death saplings, wherein we set the binary response to one for pig-induced deaths and zero other-deaths. [This last model assessed if the effects from pigs significantly differed from background mortality](#). By using three complimentary tests (pig-induced deaths vs. survivors; other-deaths vs. survivors; pig-induced deaths vs. other-deaths) we were able to determine whether the effects of explanatory variables affected the odds of dying from each type of mortality and if the effect size magnitude differed.

[Our four hypotheses are tested in each model by assessing the significance of four key covariates. Firstly, to test the hypothesis that pig mortality varied between habitats, we included the abiotic habitat type where each tagged sapling found in a nest was located in all models. Secondly, to assess if pigs caused higher mortality in clumps, we included the heterospecific density around each sapling in all models. Thirdly, to assess if pigs caused conspecific negative density dependence \(CNDD\), we included the conspecific density around each sapling in all models. And finally, to assess if non-pig-related deaths showed patterns of CNDD, we again included the conspecific density around each sapling.](#)

In all GLMMs, we accounted for spatial autocorrelation among nearby stems by including a random intercept for each 10 X 10-m subplot (N = 2196). This fine-scale of spatial autocorrelation was chosen to allow for shared responses within localized areas (Johnson et al. 2017; McFadden et al. 2019). We assessed if there was support for interactions using model selection by comparing Akaike information criterion (AIC) values. There was no support for interactions among variables in the models presented in this study. We included a set of biotic and abiotic factors that have been shown to be correlated with differences in spatial patterning and mortality in other studies of tropical forest seedlings or saplings [35–37] and may be linked to pig nesting preferences. All models included the sapling dbh as a predictor of mortality because previous work has shown pigs prefer smaller saplings (Luskin et al. 2017). To address whether certain life history strategies were more prone to pig induced mortality, we included whether the species was pioneer versus a seral or late-successional species, as identified by Davies et al. (2003), as since these species are known to have higher recruitment and mortality rates. To assess significance [of predictors included in the ~~in~~ GLMMs](#), we used Satterthwaite approximations for the degrees of freedom [and report z-values and P-values \(lmerTest package in r \[38\]\). Degrees of freedom are not provided in the lme4 package for GLMMs for conceptual reasons, although it should be noted that our sample sizes were very large \(34950 stems\) and we limited our predictors to <10 variables that included <20 total factor levels.](#)

Predictors of sapling mortality

In each GLMM, we tested for whether pigs targeted sapling clumps by including the heterospecific sapling abundance within 5-m radius neighbourhoods (calculated for each sapling) and we tested for CNDD by including the conspecific sapling abundance in the 5-m radius neighbourhood. We tested if common species faced higher mortality by including the species stand-level abundance (total saplings of each species in the 25-ha study area).

In each GLMM, we assessed if local abiotic factors (elevation, slope, and soil habitat type) were associated with the odds of mortality (table 1; figure 1). For the soil type variable (descriptions in Study Site section), dry alluvial soil was included as a categorical variable and compared to the other three soil types combined (grouped), because the other three soil types showed no effect on mortality and there was no significant variation among them. We used AIC model selection to confirm reducing the levels of this categorical variable improved model fit. In a separate set up models, we included the 10 most abundant sapling families as predictors of mortality, which included Dipterocarpaceae and Myristicaceae. To avoid overfitting, the 10 common families were assessed relative to the mean of all other families combined.

Tree diversity in quadrats with and without pig nesting

We assessed changes in sapling density and diversity between 1995 and 2000 within 400 m² quadrats (20 x 20 m; hereafter ‘quadrats’) using linear regressions (LR). The LR response variables were differences in sapling density, species richness or species evenness between the censuses, measured for each 400 m² quadrat (N = 554). We included a dummy variable (0 or 1) to assess if changes in density and diversity differed between quadrats with ≥1 pig-induced sapling deaths versus those with zero pig-induced sapling deaths.

Determining if rare species were spared from pig nests

We assessed if the composition of saplings in pig nests was representative of the community using the Wilcoxon rank sum test comparing the species abundance distributions among species found within nests differed the those for species that were never found in nests. We evaluated if the actual species richness found within nest saplings differed from a random sample of the entire 1995 baseline community using the Kolmogorov-Smirnov test. For the latter, we created a null distribution of expected species richness among nest saplings – assuming pigs harvested randomly - by simulating 10000 random subsets of 1,672 stems (number of stems recovered from pig nests) taken from the full community of 34,950 saplings. All statistical analyses were conducted using the statistical program r version 3.5.1.

RESULTS

Tree sapling mortality

There were 34,950 saplings (1.0-1.5 cm dbh) alive in 1995 from 661 species in the 22.08-ha study area. In the 2000 census, 8,911 (25.5%) had died or were broken below measurement height (assumed to have died), of which 1,672 (18.76%) were found in pig nests (‘pig-induced deaths’) in the 1996 and 1998 surveys and 7239 (81.2%) were not associated with pig nests in these two years (‘other-deaths’).

Pigs nesting removed 6.24% of stems from dry alluvial soil habitats and 2-3% of stems in each other habitat. There were higher sapling densities in lower elevations, flatter areas, and in dry alluvial soils (table 1, figure 1 & S2). Dry alluvial soils also contained more common species than the other habitat types, as measured by the average stand-wide abundance of stems found in each soil type. [Pielou](#) species evenness was also 6.9-8.7% lower in alluvial habitats than the other three soil types (LM: [df = 34948, t = -109.4, P < 0.001](#)). Species stand-wide abundance was positively correlated with both conspecific and heterospecific densities, meaning that common species are more likely to be found in [clumps-denser areas of saplings](#) (table 1 & figure S2).

Pig-induced mortality patterns differed from other sources of mortality

Within the 1.0-1.5 dbh size class of saplings, those with smaller dbh were significantly more likely to suffer pig-induced deaths ([GLMM coefficient: z-value = -20.234, P < 0.001](#) in GLMM 1) and other-deaths ([z = -17.744, P < 0.001](#) in GLMM 2; figure 2; table S5). Sapling pig-induced deaths showed clear abiotic associations revealed by positive relationships with topographic position (slope), elevation, and dry alluvial soil habitats ([z < -10 and P < 0.001](#) for all three), and all three abiotic variables were stronger predictors (larger parameter magnitude) of pig-induced deaths than other deaths ([z > 4 and P < 0.001](#) for all three). The effect of being a pioneer species was not a significant predictor of pig-induced deaths ([z = 1.840, P = 0.066](#)) but pioneers did have greater odds of other-deaths ([z = 3.148, P = 0.002](#)).

The GLMM 1 results (pig-induced deaths versus survivors) revealed that higher neighbourhood conspecific densities increased the odds of pig-induced mortality (CNDD; [z = 4.760, P < 0.001](#)). When including abiotic habitat variables, which were correlated with heterospecific neighbourhood densities (figure S2), then there was no significant effect of heterospecific density on the odds of pig-induced mortality ([z = 1.165, P = 0.244](#); table S5). A reduced version of GLMM1 that omitted abiotic variables revealed that neighbourhood heterospecific density increased the odds of pig-induced mortality ([z = 2.899, P = 0.034](#); figure s3; table S6). Likewise, a reduced version of GLMM1 including only stem diameter and species abundance as fixed effects indicated that species with higher stand-level abundance faced higher odds of pig-induced mortality ([z = 3.911, P = 0.019](#)). The significance of these parameters in reduced models but not full models is explained by conflation of habitat variables (elevation, slope, and soils) with neighbourhood heterospecific density and species stand-level abundance (figure 2).

[Other work as suggested that CNDD may vary with species abundance \[20\]. We tested this by including an interaction term between neighbourhood conspecific density and species stand-level abundance GLMM1. We found no support that CNDD from pigs varied with species stand-level abundance when controlling habitat covariates \(z = 0.098, P = 0.922\) or excluding habitat covariates \(z = 0.398, P = 0.690\).](#)

The GLMM 2 results (other-deaths versus survivors) also revealed that neighbourhood conspecific density increased the odds of pig-induced mortality ([z = 3.051, P = 0.002](#)), albeit this effect size was significantly smaller than for pig-induced deaths ([z = 2.886, P < 0.001](#)). However, increasing heterospecific neighbourhood densities reduced odds of mortality ([z = -7.967, P < 0.001](#)), indicating dense neighbourhoods had higher odds of

survival, and which was the opposite direction as its effect on pig-induced mortality (figure 2; table S5). Stand-level species abundance was negatively associated with odds of other-deaths ($z = 3.068$, $P = 0.002$), suggesting common species suffer lower odds of mortality, again the opposite effect as for pig-induced mortality. Most covariate estimates significantly differed between pig-induced deaths and other deaths ($P < 0.02$ for all comparisons in table S5 & S6), showing pigs produced distinct patterns of sapling mortality.

Mortality among families

While we did not predict that pigs were selective for their nests based on tree phylogenetics, we also tested this assumption. If pigs selected specific families in their nests, this might cause differences in the mortality rates due to pigs versus other-deaths among families. The results revealed that the Dipterocarpaceae mortality rate was higher than the plot-wide average mortality rate for both pig-induced deaths and other-deaths ($z = 4.312$, $P < 0.001$), but this effect did not differ significantly between cause of death ($z = 0.612$, $P = 0.234$). There were few significant differences between pig-induced deaths versus other-death-saplings, with two exceptions: Myristicaceae was more likely to suffer pig-induced deaths than other-deaths and Rubiaceae was slightly less likely to suffer pig-induced deaths than other-deaths (both $P < 0.001$; table S7). Including family in the GLMMs models with sapling densities and abiotic factors did not alter the direction of the previously reported effects or the significance at $P < 0.05$ level for any previously reported results.

Diversity in quadrats with and without pig nesting

Of the 554 quadrats in the sample area, Pielou evenness increased in all quadrats, but increased 105% more in the 291 quadrats with pig-induced deaths than without pig-induced deaths (LR: $df = 1101$, $t = 4.02$, $t = -13.977$, $P < 0.001$; table S7). In the initial census, quadrats that latter suffered pig-induced deaths were 19.8% more dense (LR: $df = 1104$, $t = -12.06$, $P < 0.001$), had 9.1% higher species richness (LR: $df = 1104$, $t = -11.27$, $P = 0.001$) and had 1.5% lower Pielou evenness (LR: $df = 1104$, $t = 4.25$, $P < 0.001$) than quadrats without pig-induced deaths (figure 3; table S7). Between the two censuses, quadrats with pig-induced deaths also had significantly larger declines stem density and species richness and significantly larger increases in evenness (LR: all $P < 0.01$). Specifically, sapling density declined from 1995 to 2000 in both quadrat groups, but the decline was 38.1% larger in quadrats with pig-induced deaths (LR: $df = 1101$, $t = -5.435$, $P < 0.001$). Among the quadrats with pig-induced deaths, sapling species richness only declined 2.72% despite a 27.8% decline in mean sapling abundance during the study period.

Rare species were spared from pig nests

Of the 661 species of saplings in 1995, only 322 species were found in nests, statistically fewer than expected by chance (figure 3e), and the species stand-level abundance distributions differed between nest-species and those species never used in nests (Wilcoxon rank sum test, $P = 0.002$; figure 3f). Further, abundant species suffered more total pig-induced deaths and higher per-capita pig-induced deaths than rarer species (Kolmogorov–Smirnov test, $d = 0.114$, $P < 0.001$; figure 6c). The average stand-level sapling abundance for species suffering pig-induced deaths was 452.3 stems, 17.8% higher than the average abundance of a surviving stem (384 stems), and 16.4% higher than other-dead saplings (388.5 stems; LR: $df = 34948$, $t = 10.197$, $P < 0.001$).

DISCUSSION

Our study illustrates that wildlife can alter tropical tree diversity through stand-scale and neighborhood-scale habitat preferences. Specifically, at the stand scale, we found native wild pigs' habitat selection for nest building overlapped with the habitat associations of common tree species and areas with denser saplings. [This results in higher weighted average species evenness across habitats. Rarer species from smaller habitats may not replace those common stems killed by pigs, which is likely due to habitat filtering, so this mechanism may not support coexistence.](#) At the neighborhood-scale ([e.g. within a single habitat](#)), pig-induced mortality was associated with conspecific density thereby inducing conspecific negative density dependence (CNDD), which increased species evenness and may support a coexistence, [in the same way that Janzen-Connell effects support coexistence.](#) These results are ecologically significant because pig nesting was responsible for at least 18% of sapling mortality at our site, quadrats with nest mortality was associated with 105% greater increases in species evenness than quadrats without nest mortality. [While our study focused on the processes explaining shifts in diversity from 2000-2005, another study from site found sapling species evenness increased consistently between 1986-2010 \[23\], suggesting pigs' impacts on diversity are a persistent feature of this forest.](#)

Pigs' habitat preferences for nest building were logical for safe and efficient construction, and thus supported our hypotheses 1-3. First, pigs preferred flat dry habitats, which would intuitively reduce the likelihood of nests flooding or toppling. As a result, pig-induced sapling mortality was more severe in lower and flatter locations and in unflooded alluvial soil habitats, which were the same habitats that hosted higher sapling densities and higher proportions of common species in our site. [Common species also had higher per capita rates of mortality due to pigs because of their habitat associations and not clumping patterns.](#) Second, pig-induced sapling mortality was also associated with local sapling densities, which would be suitable for optimal forging of nest materials. Third, as tree sapling of the same species are often aggregated due to dispersal limitation and fine-scale habitat filtering [16–19,37], we predicted and found that stems with nearby conspecifics were more likely to suffer pig disturbances. Taken together, pigs' stand-level and neighbourhood-level nesting preferences both promoted species evenness measured at scales of 0.04 to 1.0 ha (figure 3f). [Pigs also had a small negative effect on species richness, which only slightly declined by 2.72% due to sampling effects \(fewer total stems\).](#)

Pig nesting, CNDD, and tree diversity

Local-scale CNDD resulted from the interaction of pig disturbances and the underlying tree spatial aggregation patterns, and not species selectivity at our study site. [Since pigs kill saplings, they can be considered as enemies within the framework of the Janzen-Connell Hypothesis \(JCH\). However, This the mechanism pattern of enemy-mediated CNDD by pigs is distinct from most realizations of Janzen-Connell Hypothesis JCH,](#) which posits that - as a plant species density increases - populations of its dispersal-limited and host-specific arthropods and fungi enemies increase [8]. Since our focal enemies (pigs) are a generalist mobile omnivore, [and tree mortality did not result from their selectivity, nor do pig populations increase with the host species saplings abundance. Therefore,](#) our case represents a new variety of enemy-mediated CNDD [within the broader JCH](#)

~~framework on the spatial patterns of enemy attack rates~~, ~~that can also supports coexistence~~. Taken together, our study provides a robust and intuitive example of how wildlife can induce CNDD that is missing in the literature. Further, it is also interesting in that it shows how indirect processes can produce CNDD, which complements the more widely observed direct processes from ~~Janzen–Connell~~JCH effects (host-specific tree enemies) and intra-specific competition [39].

Positive density dependence among non-pig afflicted saplings

Pig-induced sapling mortality showed opposing patterns compared to mortality from other sources. This illustrates wildlife can inflict fundamentally different processes, and not just reinforce other mortality processes. For example, both pig-induced mortality and other-sources of mortality showed significant CNDD (hypothesis 4), so in this case pigs would reinforce CNDD processes that might have arisen due to enemy-mediated JCH effects or intra-specific competition [35]. However, while pig-induced mortality was higher in areas with more heterospecifics, other sources of mortality actually showed lower odds of mortality in clumps (heterospecific *positive* density dependence), which – in the absence of pig nesting - would cause increased spatial aggregation among the sapling community through time. This finding could be due to beneficial effects of shared soil fungal networks among ectomycorrhizal trees that helps maintain their local dominance [40]. Other sources of mortality were stronger for common than rare species at the stand-level, which would erode species evenness in the community. Thus, while pig-inflicted mortality reduced sapling aggregations and supported diversity, the other sources of mortality induced the opposite trends.

Are pig impacts on tree communities biologically significant?

The magnitude of diversity change was large relative to a similar dipterocarp forest study in the region at Lambir Hills in Borneo [37]. Sapling densities in the first Pasoh census (1985) were comparable to Lambir but the magnitude of diversity changes we observed were larger than for other than Lambir. We found that Pielou's evenness increasing by 0.49% in 20-m neighborhoods around pig-induced death-saplings over five years (equivalent to 9.8% per century). Further, our results likely underestimate the effect of pig-induced increases on tree sapling evenness for three reasons. Firstly, most stems used in nests are <1 cm dbh so, by focusing on larger saplings, we only captured a fraction of the total pig-induced mortality [23]. Secondly, a considerable number of tags from pig-induced death-saplings were not found in the pig nests, as some would have fallen off when the stem was snapped and carried to nests. This was apparent because the number of saplings >1 cm found in nests was much higher than the actual number of tags recovered, meaning we underestimated all pig-induced deaths. Thirdly, nest surveys were not available for 1997, 1999 and 2000 and consequently, saplings labeled 'other-deaths' likely include many pig-induced deaths from these years yielding another source of underestimation. The issues of lost tree tags and the impacts of pigs during unsampled years may explain why sapling densities declined in quadrats without recorded pig-induced deaths and make our estimates of pig influence conservative.

Longer-term implications

We do not suggest that pig nesting disturbances observed at Pasoh are necessarily representative of other sites, or that the observed impacts at Pasoh will have lasting effects on diversity, ~~because~~because pig densities are elevated at our site and wildly fluctuate between decades [23]. At Pasoh, the direct management of pigs

(culling) ~~or and~~ removal of oil palm food subsidies ~~could reduce~~s their densities and reproductive activity, thereby reducing pig nesting and the impacts on saplings [23]. ~~(Luskin et al. 2014)~~. There is also the potential for feedbacks from pig nesting to mitigate changes reported here over longer periods. For example, as pig nesting thins the understory, this could reduce understory plant competition, which in turn could aid future tree regeneration and produce unclear long-term outcomes that depend on colonizing species. Nesting damage increased species evenness in the short term in our study, and only had small negative effect on richness, but severe ongoing pig-inflicted mortality would eventually reduce richness due to the sampling effect. We also considered that stems found in nests were killed while in fact, many stumps created by pigs resprout, although resprouting stumps face much higher mortality than unbroken stems [27,41]. We also narrowly focused on trees in this study, pig nesting has also been shown to increase the relative abundance of lianas at Pasoh, as pigs tend to avoid using liana saplings for nests, likely due to the difficulty breaking their stems [42] and lianas can have a negative impact on tree survival and growth [43]. Finally, tree dispersal syndromes are linked to sapling distributions, with ballistic and wind-dispersed species being more aggregated than vertebrate-dispersed species [17]. Many dominant tree species in the Neotropics tend to be animal dispersed, while Southeast Asian forests are more dominated by wind-dispersed species [37,44]. Thus, wildlife induced-CNDD may disproportionately affect common species in Southeast Asia (as we observed) but not the Neotropics.

Conservation implications

The findings presented here show that elevated pig populations can affect forest diversity over a relatively short time, which may have regional and global conservation repercussions for the maintenance of tree diversity in protected areas. Research on ecological cascades has documented many links between altered wildlife and vegetation dynamics [3], but not yet to how this alters tree HNDD and CNDD. Our previous work from the site has shown that oil palm provides food subsidies to crop-raiding pigs and this triggers ecological cascades that reach the interior of protected areas [23]. This study extends this work in showing that subsidy cascades can also influence CNDD and tree diversity. Currently, there are ~7 Mha of oil palm and ~15 Mha of forest in Malaysia, with most forests being fragmented and close to oil palm plantations [45,46]. Pigs are now over-abundant in many forests in Southeast Asia [21,22,24,25] and pigs are invasive in other oil palm growing regions [26], making cascading effects of these paired problems a potential global conservation issue. Mitigating the impacts from oil palm and pigs on forests could be accomplished through landscape planning or managing pigs, such as through culling or controlled hunting. On the contrary, defaunated forests may be missing these key wildlife disturbances that contribute to the maintenance of hyperdiverse plant communities.

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AUTHORS' CONTRIBUTIONS

M.S.L. designed the study and analysed the data. K.I. conducted the pig nest surveys, Y.T.L. and S.J.D. manage the tree census database, and D.J.J. assisted with the data analysis. M.S.L., S.J.D. and D.J.J. wrote the paper. All authors contributed to the final version.

DATA ACCESSIBILITY

Nesting data is available via the Dryad Digital Repository <https://dryad.XXXX> (Luskin, Ickes, Yao, & Davies, 2019) and tree census data is available at <https://forestgeo.si.edu/sites/asia/pasoh>.

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Soil habitat	Total stems in habitat	Stems found in pig nests	% stems found in pig nests	Elevation (mean)	Slope (mean)	Stand-wide species abundance (median)	Species richness	Pielou species evenness
Wet alluvial	8034	237	2.950	81.65	1.15	124	533	0.849
Dry alluvial	20207	1261	6.240	82.88	0.95	234	575	0.791
Laterite-derived	4288	120	2.799	89.80	5.14	139	439	0.866
Shale-derived	2421	54	2.230	90.84	4.25	118	362	0.877
<i>Totals</i>	<i>34950</i>	<i>1672</i>	<i>4.784</i>					

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Table 1 Characteristics of sapling communities in each of the four main soil habitats. Stand-wide species abundance is the total number of saplings 1-1.5 cm dbh in the 25 ha plot for each species, and the table shows the median value among stems located in each habitat.

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Figure 1 Locations of pig nests, hypotheses about pig nesting habitat preferences, and habitat characteristics of sapling that were found in nests. (a) Locations of pig nests (black points) in the 25 ha study area, colored by soil habitat type, with legend matching colors in panels d and e). In the inset, local sapling neighborhoods are shown with tree species represented by different colors. Hypotheses (H1-H4) are described in the text and table S1. (b) The 33,326 sapling stems that were not used in pig nests, plotted in elevation-slope habitat niche-space and colored by soil types (matching colors in panels d and e). (c) Wet and dry alluvial soils are flat low-lying areas, laterite-derived and shale-derived soils are found on hills. (c) The habitat conditions in the initial census for the 1,672 stems that were later recovered in pig nests, showing a clustering in low elevation, low slope sites with dry alluvial soils (orange color). (d) Mean sapling density in different in soil habitats. Letters indicate significant differences at the $P < 0.05$ level assessed using LMMs. (e) Average species stand-wide abundance for stems found in different soil habitats, showing dry alluvial soils contain more common species.

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Figure 2 Predictors of sapling mortality due to pigs (orange) versus other sources, assessed with an individual-based mortality model (GLMMs). Odds ratios below 1 indicate reduce odds of mortality, for 34,950 saplings alive in 1995 being found in pig nests in 1996 or 1998 ($N = 1672$) versus stems that died for other reasons ($N = 7285$). Values are the GLMM coefficient estimates and errorbars show 95% CI (full model output is presented in table S4). Closed circles show results with $P < 0.05$ and open circles show results with $P > 0.05$. All continuous variables were scaled (mean of 0 and sd of 1). Heterospecific and conspecific densities are measured within 5-m radius neighbourhoods of every stem. As an example of how to interpret the terms, the negative stem diameter estimates indicate that larger stems had lower odds of mortality, and this relationship was significantly stronger for pig-induced deaths than other-deaths.

Figure 3 Impacts on pig nesting on tree sapling compositions and diversity. Sapling density (a), species richness (b), and Pielou species evenness (c) in 400 m² quadrats in 1995 and 2000, separated by those quadrats with at least one pig-induced death-sapling (N = 293; orange) versus quadrats with no known pig-induced deaths (N = 261; green). Letters indicate significant differences at the $P < 0.05$ level. (d) Species abundance distributions of the 339 species found in nests (green histogram) versus the 332 that were never found in nests (orange histogram; Kolmogorov–Smirnov test, $d = 0.114$, $P < 0.001$). The histogram area for each grouping is equal to one. (e) The predicted number of species that would be found in pig nests in our study (grey histogram) versus the actual number (322 species, orange; Wilcoxon rank sum test, $P = 0.002$). The grey histogram is the null expectation produced by random drawing 1,672 stems (actual tags recovered from nests) from the 34,950 possible stems available in the in the 20.08 ha study area. (f) Changes in Pielou's species evenness, measured in square subplots. We used LMM to test if the change in diversity differed from zero and all four subplot sizes showed highly significant differences ($P < 0.001$ for all).