Research

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

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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 and nesting 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. Pigs (*Sus scrofa*) are abnormally abundant at the site due to food subsidies in nearby farmland and they construct birthing nests using hundreds of tree saplings. We tagged 34 950 tree saplings in a 25 ha plot during an initial census and assessed the source mortality by recovering tree tags from pig nests ($n = 1672$ pig-induced deaths). At the stand scale, pigs nested in flat dry habitats, and at the local neighbourhood scale, they nested within clumps of saplings, both of which are intuitive for safe and efficient nest 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 m^2 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 from 1996 to 2010, which is unsustainable. We suspect pig nesting is an important feature shaping tree composition throughout the region.

1. 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 (greater than 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 as 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's 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 that 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 greater than 1 kg (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-month 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 behaviours 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 the 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 depend on the underlying plant community composition. To better understand the role wildlife may play in shaping tree composition, we examined (i) if the spatial patterns of wildlife disturbances 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 2). 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]. In Southeast Asia, native pig species often subsidize their omnivorous diet by crop raiding on fruits in oil palm plantations, leading to much higher densities than in interior forest areas [22–25]. Pigs can suppress tree regeneration through seed predation, rooting and seedling trampling [22,26] 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 (figure 1). A single pig nest can include hundreds of tree saplings collected from a small area (approx. 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 to 2010 [22], 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-year 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 electronic supplementary material and illustrated in figure 2):

(1) Pigs nest in abiotically defined habitats (dry flat areas). If these preferred nesting areas overlap with the 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 (greater than 10 ha).
(2) At the local neighbourhood scale (less than 1 ha), pigs choose nesting sites where there are many saplings (clumps) to efficiently construct their nests. Saplings with higher neighbourhood 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 neighbourhood densities may face higher risk of mortality from pigs. This will cause 'pig-induced CNDD' and increase neighbourhood scale species evenness.

2. Methods

(a) 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

Figure 1. The birthing nest of a native wild boar (*S. scrofa*) at the Pasoh Research Forest in Peninsular Malaysia. This study documented how nesting disturbances were associated with the homogenization of tree sapling densities and increases in species evenness. (Online version in colour.)
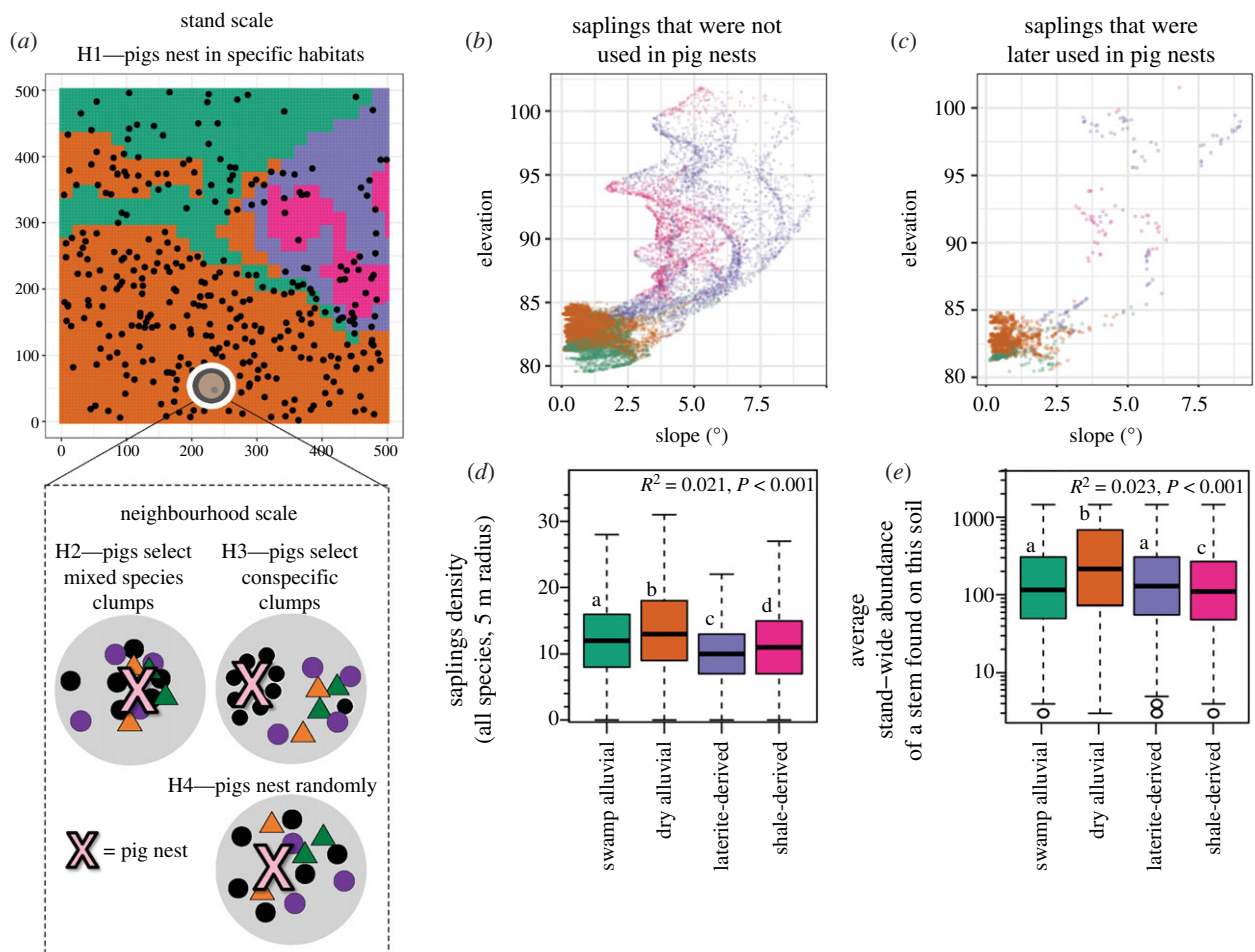

Figure 2. Locations of pig nests, hypotheses about pig nesting habitat preferences and habitat characteristics of saplings that were found in nests. (*a*) Locations of pig nests (black points) in the 25 ha study area, coloured by soil habitat type, with legend matching colours in *d* and *e*. In the inset, local sapling neighbourhoods are shown with tree species represented by different colours. Hypotheses are described in the text and electronic supplementary material, table S1. (*b*) The 33 278 sapling stems that were not used in pig nests, plotted in elevation-slope habitat niche-space and coloured by soil types (matching colours in *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 1672 stems that were later recovered in pig nests, showing a clustering in low elevation, low slope sites with dry alluvial soils (orange colour). (*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. (Online version in colour.)

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. Habitats defined by dry alluvial soils were flat and unflooded, potentially suitable making them most suitable for pig nest construction.

soil habitat	total saplings in habitat (1995)	stems found in pig nests (1995–2000)	sapling density in 1995 (ha^{-1})	% stems found in pig nests	elevation (mean)	slope (mean)	stand-wide species abundance (median)	species richness	Pielou species evenness
wet alluvial	8034	237	1551	2.950	81.65	1.15	124	533	0.849
dry alluvial	20 207	1261	1687	6.240	82.88	0.95	234	575	0.791
laterite-derived	4288	120	1319	2.799	89.80	5.14	139	439	0.866
shale-derived	2421	54	1441	2.230	90.84	4.25	118	362	0.877
totals	34 950	1672							

50 ha forest dynamics plot (FDP) established in 1985 [30]. The plot is in the centre of the reserve, greater than 1.35 km from any edge. Elevation within the 50 ha plot ranges from 80 to 110 m.a.s.l. 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 tapirs (*Tapirus indicus*), sun bear (*Helarctos malayanus*) and a number of predatory cat species including leopards (*Panthera pardus*) [22]. The seed-dispersing community has not appreciably changed from 1986 to present [22]. However, there is an over-abundance of native pigs (*S. scrofa*), whose densities were estimated from distance sampling at 27–47 individuals km^{-2} during the study period [23].

(b) Tree sapling censuses

All tree stems greater than or equal to 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 [22,28]. We categorized 1995 saplings into three groups: (i) 'survivors' (saplings with dbh ≥ 1 cm in the 1995 and 2000 censuses); (ii) 'pig-induced mortality' (saplings with dbh ≥ 1 cm in the 1995 whose stem tags were found in pig nests); and (iii) 'other deaths' (saplings in the 1995 that were marked 'dead' or 'missing' in the 2000 census but not found in pig nests).

(c) Pig nest surveys

We identified pig-induced mortality by excavating the tree tags from the 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 (s.d.: 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 5 years between censuses, the other deaths include some stems used for pig nesting in unsampled years (electronic

supplementary material, 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. These locations are similar since saplings are only taken from an area of 244 m^2, with most stems coming from within a 5 m radius around the nest site [28]. 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].

(d) Tree sapling mortality analyses

We tested our three hypotheses about the impact of pig disturbances on sapling mortality using individual-based generalized linear mixed models (GLMMs). Specifically, we compared the likelihood of saplings being found in pig nests (pig-induced deaths) versus 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 centred on the mean and standardized by 1 s.d. 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 1 s.d. 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, (GLMM2) other deaths versus survivors, wherein we set the binary response one for other deaths and zero for survivors and (GLMM3) pig-induced deaths versus other deaths of 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. All GLMM models contained the same set of predictor variables so they could be compared using model selection.

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 (elevation, slope and soil habitat type) where each tagged sapling found in a nest was located in all models. We assessed if local abiotic factors were associated with the odds of mortality (table 1 and figure 2). For the soil type variable (descriptions in the 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 and we used AIC model selection to confirm reducing the levels of this categorical variable improved model fit. Secondly, to assess if pigs caused higher mortality in clumps, we included the hetero-specific sapling abundance within 5 m radius neighbourhoods (calculated for each sapling) 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. 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).

All models included the sapling dbh as a predictor of mortality because previous work has shown pigs prefer smaller saplings [22]. 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. [29], as since these species are known to have higher recruitment and mortality rates. We did not consider how species birth, survival or intrinsic growth rates (r) affected mortality from pigs versus other sources, as this was not directly related to our hypotheses.

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 the 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 [32]). 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 (34 950 stems) and we limited our predictors to less than 10 variables that included less than 20 total factor levels.

In all GLMMS, we accounted for spatial autocorrelation among nearby stems by including a random intercept for each 10 × 10 m subplot ($n = 2196$) to allow for shared responses within localized areas [19,33]. We choose not to include species-level random effects in models presented in the main text because we had no predictions about pigs being selective. Instead, we tested if pig-driven mortality could be understood relative to their environment, so we considered how the likelihood of mortality of stem to be predicted by its abiotic and biotic neighbourhood and not species (electronic supplementary material, table S1 and box S1). We note there are also technical issues when modelling species-level mortality with habitat or neighbourhood density, since all three variables are highly conflated (figure 2; electronic supplementary material, figures S2 and S5). As a result, the species-level random effects absorb the variation in mortality among conspecifics located in different habitats or densities, causing the models to become uninformative for our main hypotheses. Therefore, we present results including species-level random effects in the electronic supplementary material.

(e) 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 × 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 greater than or equal to 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 [34]. 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 [35].

(f) 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 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 10 000 random subsets of 1672 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 v. 3.5.1.

3. Results

(a) 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, 8911 (25.5%) had died or were broken below measurement height (assumed to have died), of which 1672 (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 and figure 2; electronic supplementary material, figure 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: d.f. = 34 948, $t = -109.4$, $p < 0.001$). 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; electronic supplementary material, figure S2).

(b) 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 3; electronic supplementary material, table S5). Pig-induced sapling 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
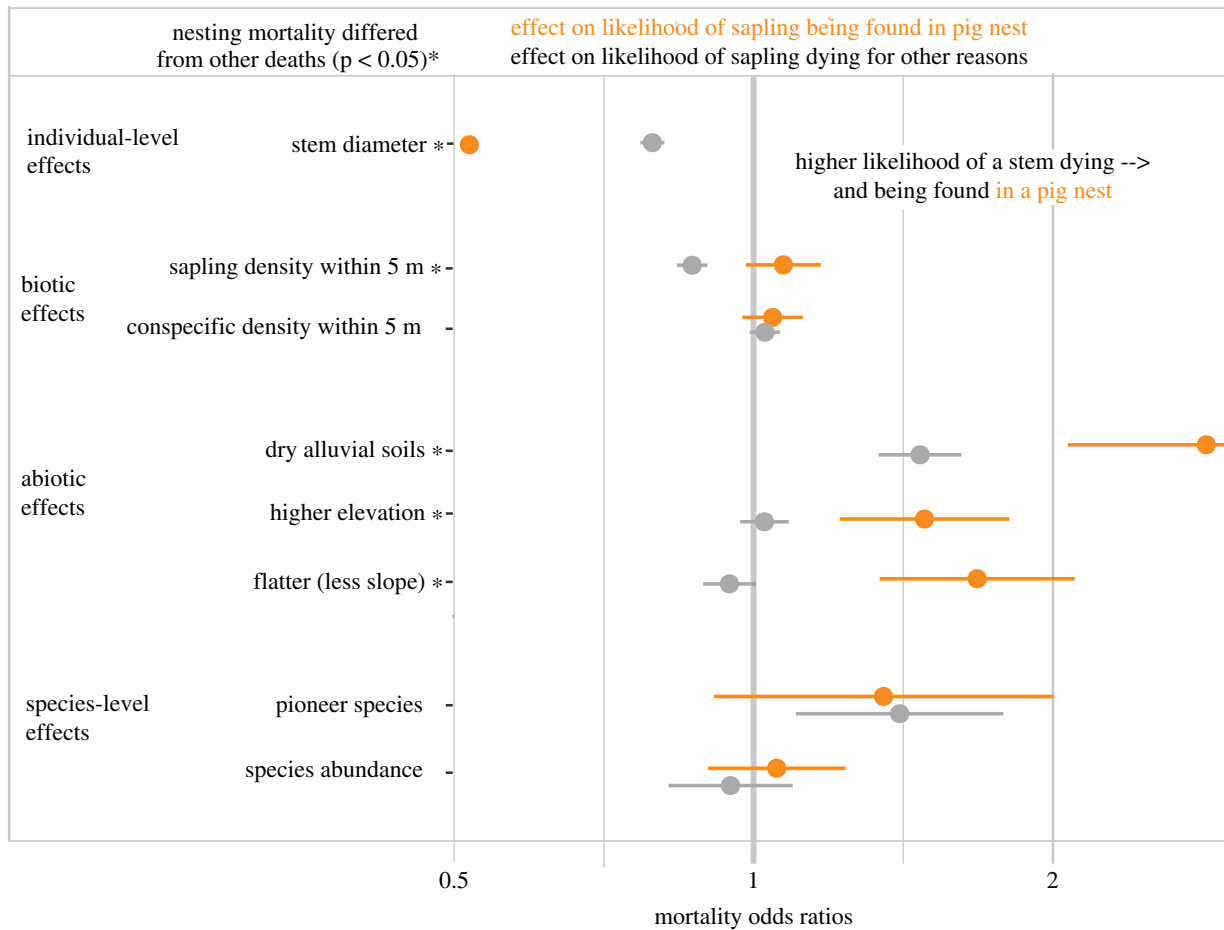
Figure 3. Predictors of sapling mortality due to pigs (orange, GLMM1) versus other sources (GLMM2), assessed with an individual-based mortality models with random effects to account for spatial pseudoreplication. Odds ratios above 1 indicate increased mortality among the 34 950 saplings. There were 1672 stems found in pig nests in 1996 or 1998 and 7285 stems that died for other reasons. Values are the GLMM coefficient estimates and error bars show 95% CI. Closed circles show results with $p < 0.05$ and open circles show results with $p > 0.05$ for the GLMM1 and GLMM2. All continuous variables were scaled (mean of 0 and s.d. of 1). Heterospecific and conspecific densities are measured within 5 m radius neighbourhoods of every stem. Significant differences between the variables were assessed using GLMM3 (pig-induced deaths versus other deaths) and is noted the asterisk next to the variable name. As an example of how to interpret the terms, the negative stem diameter coefficients indicate that larger stems had lower chance of dying, and this relationship was significantly stronger for pig-induced deaths than other deaths (denoted by the asterisk). Full model output is presented in electronic supplementary material, table S4. (Online version in colour.)

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 GLMM1 results (pig-induced deaths versus survivors, including abiotic habitat variables) revealed that higher neighbourhood conspecific densities increased the odds of pig-induced mortality ($z = 4.760$, $p < 0.001$). There was no significant effect of heterospecific density on the odds of pig-induced mortality ($z = 1.165$, $p = 0.244$; electronic supplementary material, table S5) because heterospecific neighbourhood densities were correlated with abiotic habitat variables (electronic supplementary material, figure S2). A reduced version of GLMM1 that omitted abiotic variables revealed that neighbourhood heterospecific density increased the odds of pig-induced mortality ($z = 2.899$, $p = 0.034$; electronic supplementary material, figure S3 and table S6). A reduced version of GLMM1 including only stem diameter and species abundance also suggested 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; electronic supplementary material, figure S2).

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 other deaths (GLMM2: $z = 3.051$, $p = 0.002$), albeit this effect size was significantly smaller than for pig-induced deaths (GLMM3: $z = 2.886$, $p < 0.001$). However, increasing heterospecific neighbourhood densities reduced odds of mortality (GLMM2: $z = -7.967$, $p < 0.001$), indicating dense neighbourhoods had higher odds of survival, and which was the opposite direction as its effect on pig-induced mortality (figure 3; electronic supplementary material, table S5). Stand-level species abundance was negatively associated with odds of other deaths (GLMM2: $z = 3.068$, $p = 0.002$), suggesting common species suffer lower odds of mortality, again the opposite effect as for pig-induced mortality. Most
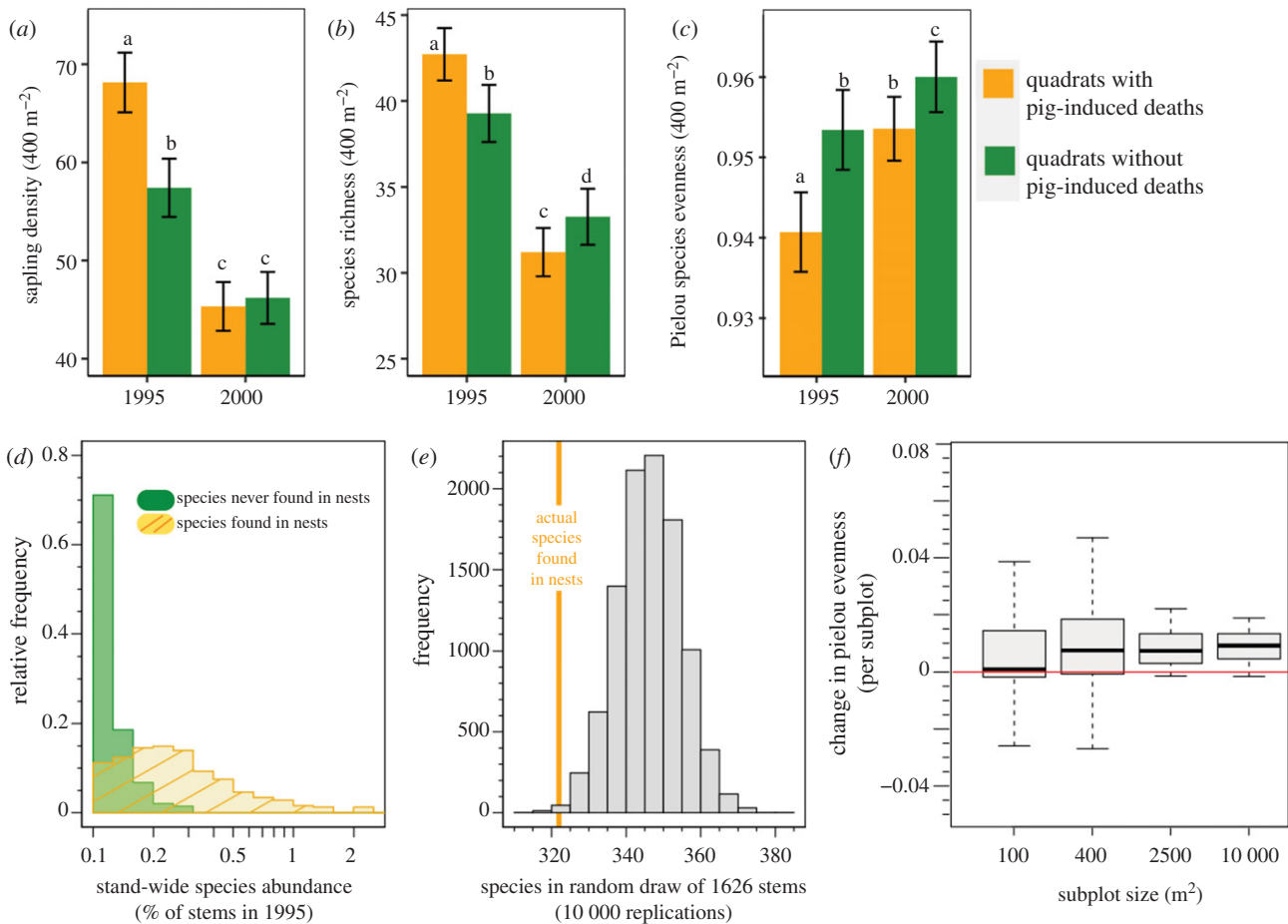
Figure 4. Impacts on pig nesting on tree sapling compositions and diversity. (*a*) Sapling density, (*b*) species richness and (*c*) Pielou species evenness in 400 m² quadrats in 1995 and 2000, separated by those quadrats with at least one pig-induced death (*n* = 293; orange) versus quadrats with no known pig-induced deaths (*n* = 261; green). Letters indicate significant differences at the *p* < 0.05 level, assessed using linear mixed models. Note, this quadrat-level summary of community composition changes is different than the previous individual-level mortality models (GLMMs 1, 2 and 3). (*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 1672 stems (actual tags recovered from nests) from the 34 950 possible stems available in the 22.08 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). (Online version in colour.)

covariate estimates significantly differed between pig-induced deaths and other deaths (GLMM3: *p* < 0.02 for all comparisons in electronic supplementary material, table S5 and S6), showing pigs produced distinct patterns of sapling mortality.

The results were qualitatively similar when we included a species-level random effect into GLMMs 1, 2 and 3, except conspecific density was no longer significant (electronic supplementary material, figure S4). However, this change was only due to strong correlations between the species-level random effects (differences in mortality rates) and conspecific densities (electronic supplementary material, figure S5). The interpretation is that species aggregated in clumps had higher mortality from pigs, especially in dry alluvial habitat. We also re-ran the models only including data from dry alluvial habitat and found similar results showing significantly higher pig mortality for stems in both heterospecific and conspecific clumps (electronic supplementary material, figure S6).

(c) 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: d.f. = 1101, *t* = 4.02, *t* = −13.977, *p* < 0.001; electronic supplementary material, table S7). In the initial census, quadrats that later suffered pig-induced deaths were 19.8% more dense (LR: d.f. = 1104, *t* = −12.06, *p* < 0.001), had 9.1% higher species richness (LR: d.f. = 1104, *t* = −11.27, *p* = 0.001) and had 1.5% lower Pielou evenness (LR: d.f. = 1104, *t* = 4.25, *p* < 0.001) than quadrats without pig-induced deaths (figure 4; electronic supplementary material, table S7). Between the two censuses, the sapling densities declined 38.1% more in quadrats with pig-induced deaths (LR: d.f. = 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 the mean sapling abundance during the study period.

(d) 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 4*e*). 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 4f), with more abundant species suffering higher pig-induced death rates (Kolmogorov–Smirnov test, $d = 0.114$, $p < 0.001$; figure 4c). 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-death saplings (388.5 stems; LR: d.f. = 34 948, $t = 10.197$, $p < 0.001$).

4. Discussion

Our study illustrates that wildlife can alter tropical tree diversity through stand-scale and neighbourhood-scale habitat preferences. At our primary rainforest forest in Malaysia, native wild pigs removed woody and herbaceous stems in small areas to build nests. Pigs nested in flat but unflooded areas of the landscape and disproportionately utilized aggregated saplings. At the stand scale, pigs' habitat selection overlapped with the habitat associations of more common tree species, inducing higher tree mortality that 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 neighbourhood scale (e.g. within a single habitat), pig-induced mortality was associated with heterospecific and conspecific density, the latter inducing CNDD, which increased species evenness. This source of CNDD may support coexistence, but the most appropriate analogy would be similar to a high-intensity but patchy fire, as opposed to species-specific mortality from host-specific enemies within the Janzen-Connell framework.

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 [16–19,36], 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 neighbourhoods around pig-induced death saplings over just 5 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 1995 to 2000, another study from site found sapling species evenness increased consistently between 1986 and 2010 [22], suggesting pigs' impacts on diversity are a persistent feature of this forest.

(a) Pigs as tree enemies

Since pigs kill saplings, they can be considered as tree enemies, but their impacts differ from the impacts of generalist herbivores that can cause CNDD even through relatively non-selective grazing or browsing [37,38]. Most realizations of Janzen–Connell hypotheses 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) are 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 that is more akin to localized disturbances—such as a patchy fire, lightning strikes or landslides—and provides a robust and intuitive example of how wildlife can induce CNDD that is missing in the literature.

(b) 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 Janzen–Connell effects or intraspecific competition [33,39]. 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 [40].

(c) 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 less than 1 cm dbh so, by focusing on larger saplings, we only captured a fraction of the total pig-induced mortality [22]. 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 greater than 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 labelled 'other deaths' probably include many pig-induced deaths from these years yielding another source of underestimation.

(d) 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 [22]. We narrowly focused on trees in this study, but pig disturbances at Pasoh have also been shown to increase the relative abundance of lianas [41], which suppress tree survival and growth [42], and contributes to spreading invasive species [43]. Finally, we suggest 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].

(e) 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. Ongoing pig-inflicted mortality would eventually reduce richness and cause negative cascading impacts on forest. On the contrary, defaunated forests may be missing these wildlife disturbances that contribute to the maintenance of hyperdiverse plant communities.

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 greater than 1 km into the interior of protected areas [22]. This study extends this work in showing that subsidy cascades can also influence CNDD and tree diversity. Currently, there are approximately 7 Mha of oil palm and approximately 15 Mha of forest in Malaysia, with most forests being fragmented and close to oil palm plantations [44,45]. 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. The lethal onslaught of African swine fever across Asia may severely reduce pig densities in the coming years and provides opportunities for natural experiments about pigs impacts on ecosystems [46].

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