

# Individual tree damage dominates mortality risk factors across six tropical forests

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## Summary

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**Key words:** climate change, ForestGEO, modes of death, mortality risk factors, tree comorbidity, tree damage, tree mortality, tropical forests.

- The relative importance of tree mortality risk factors remains unknown, especially in diverse tropical forests where species may vary widely in their responses to particular conditions.
- We present a new framework for quantifying the importance of mortality risk factors and apply it to compare 19 risks on 31 203 trees (1977 species) in 14 one-year periods in six tropical forests. We defined a condition as a risk factor for a species if it was associated with at least a doubling of mortality rate in univariate analyses. For each risk, we estimated prevalence (frequency), lethality (difference in mortality between trees with and without the risk) and impact ('excess mortality' associated with the risk, relative to stand-level mortality).
- The most impactful risk factors were light limitation and crown/trunk loss; the most prevalent were light limitation and small size; the most lethal were leaf damage and wounds. Modes of death (standing, broken and uprooted) had limited links with previous conditions and mortality risk factors.
- We provide the first ranking of importance of tree-level mortality risk factors in tropical forests. Future research should focus on the links between these risks, their climatic drivers and the physiological processes to enable mechanistic predictions of future tree mortality.

## Introduction

Tree mortality is a key component of forest functioning and dynamics, affecting forest structure, community composition and biogeochemical cycles (Franklin *et al.*, 1987). Recent studies have reported rising tree mortality rates in forests worldwide (Allen *et al.*, 2010; McDowell *et al.*, 2020), including the tropics (Hubau *et al.*, 2020). A range of external drivers may lead to increases in tree mortality; for example increased disturbance rates, increased drought frequency or increased herbivore pressure. The underlying mechanisms of individual tree death remain poorly understood, especially in tropical forests. An improved understanding of how mechanisms act and interact to generate mortality patterns will help us to upscale from individual-level processes to global systems and better predict the future behaviour of Earth's ecosystems.

The survival of individual trees depends on a wide range of environmental, physical and physiological conditions and species differ in their responses to these conditions. Species differentially

allocate resources to traits that may confer an advantage under certain environmental conditions, with the trade-off that they may be more at risk of death under other conditions. For example, acquisitive species do well in high resource environments, but die easily in low resource conditions or following a sudden decrease of resource availability (Kobe *et al.*, 1995; Wright *et al.*, 2010). These trade-offs may be also evident across ontogeny, with trees of most species exhibiting higher mortality when small, and other species having higher mortality when large (e.g. Davies, 2001; Johnson *et al.*, 2018). This pattern of trade-offs in allocation extends to numerous potential conditions associated with elevated risk of death, from this point forwards defined as mortality risk factors or simply risks. Individual-level conditions that may superficially look negative for a tree are mortality risk factors only if they objectively increase an individual's probability of death. As a result, the same condition may be a mortality risk for some species but not others (Box 1). To translate tree-level conditions into objective risk factors we need a comprehensive

assessment of patterns of survival across a range of forest types, environmental conditions and species.

Despite the diversity of conditions that trees experience in the forest, many studies of tropical forest mortality classify the causes of death into structural vs physiological factors (Chao *et al.*, 2009; Esquivel-Muelbert *et al.*, 2020). Distinguishing between physiological and structural causes of tree death is typically inferred from the physical state of a dead tree, without considering observations before death. Trees that are found dead and broken or uprooted are assumed to have died of structural causes, whereas trees found dead and standing are considered to have died of physiological causes (e.g. Gale & Barfod, 1999; Slik, 2004; De Toledo *et al.*, 2011). By focusing on observations of dead trees, this approach cannot distinguish whether some events occurred before or after the death of the tree (e.g. trunk breakage, leaning, fungal infestation, trunk rot, etc.) and fails to consider some relevant conditions that are not measurable on dead trees (e.g. defoliation, herbivory, light limitation), or disappear rapidly as wood decomposes (e.g. lianas, stranglers, wounds, tumours) (Das *et al.*, 2016; Yanoviak *et al.*, 2019). These problems are exacerbated when the interval between censuses is long, as is common in tropical forest plot monitoring projects (e.g. Davies *et al.*, 2021; ForestPlots.net, 2021). Despite its limitations, the use of *post mortem* evaluations to infer structural vs physiological causes of death remains central to large-scale and long-term studies of tropical tree mortality (Chao *et al.*, 2009; Esquivel-Muelbert *et al.*, 2020).

An alternative to the *post mortem* evaluation is to observe the conditions of living trees, follow them over time and then assess which conditions are associated with an elevated risk of death in order to identify mortality risk factors. As this approach requires observations on many living trees and following them until death, the few studies that have assessed multiple mortality risk factors in a time-intensive way have been restricted to small sample sizes and limited geographical areas and environments (Fontes *et al.*, 2018; Aleixo *et al.*, 2019; Preisler *et al.*, 2020). Yet, to elucidate the relative importance of different factors, it is critical to simultaneously record data on a broad suite of observations of living trees and monitor their subsequent survival. By doing so, it would be possible to assess which mortality risks are most common in tropical forests (prevalence), which most elevate individual mortality (lethality) and which contribute most to overall mortality rates (impact) within and among forests (Box 1). Furthermore, by monitoring the frequency of mortality risks in living trees, it should be possible to detect increases in the frequency of mortality risks before any change in mortality.

Here, we use annual assessments of survival status and numerous tree-level conditions to identify mortality risk factors and evaluate their relative importance in tropical forests. We used 99 858 (individual × census) sets of observations, each spanning 15 conditions, collected in annual censuses between 2016 and 2020 on 31 203 individual trees of 1977 species in six tropical forests. Our overarching goal was to provide a ranking of importance of risk factors based on their impact in these tropical forests. We present and apply a new quantitative framework to assign tree mortality risk factors and thereby compare which are most important in terms of their prevalence (frequency of trees

affected), their lethality (differences in mortality between trees with and without the risk) and their total impact (proportion of total mortality that is ‘excess mortality’ associated with the risk). We also evaluated the degree to which conditions and mortality risk factors on living trees varied systematically among traditional *post mortem* assignments of modes of death (i.e. standing, broken and uprooted).

## Materials and Methods

### Study sites

This study was conducted within six large-scale (24–50 ha) tropical forest plots of the ForestGEO network; two in the Neotropics: Amacayacu (Colombia) and Barro Colorado Island (BCI, Panamá); and four in Asia: Fushan (Taiwan), Huai Kha Khaeng (HKK, Thailand), Khao Chong (KC, Thailand) and Pasoh (Malaysia) (Anderson-Teixeira *et al.*, 2015; Davies *et al.*, 2021). The sites ranged from ever-wet to seasonally dry forests, including sites affected by cyclones, fire, local landslides and droughts (Supporting Information Table S1). Sites also varied in edaphic heterogeneity, with topographic relief ranging from 20 m in Amacayacu to 250 m in KC. At each plot, all trees were mapped, measured and identified to species and topographic surveys were carried out.

### Sampling design

The study included 33 933 stems of 31 203 trees and 1977 species (2156 species × site combinations) (Table S1). In each site, we examined and followed the fate of a cohort of 4507–8464 stems (average 5655) with diameter at the point of measurement (dbh) ≥ 10 mm that were alive in the most recent complete census of the plot. Depending on the site, each tree was revisited between two and five times between 2016 and 2020 for a total of 14 one-year census intervals and 99 858 (individual × census) observations. Trees were selected based on a nested sampling design stratified by habitat and size to capture the diversity of species, the range of tree sizes, topography and other environmental features within plots. Overall, species included in our sample represented 92% of the total number of individuals in these forests. Arellano *et al.* (2021) provide extensive details on the sampling design and field methods.

### Tree-level conditions

The series of observations made on each stem and individual are described in detail in the protocol for the annual mortality surveys of ForestGEO (Arellano *et al.*, 2021). Briefly, for each tree, we recorded: (1) the survival status of the individual (dead/alive); (2) the physical state of each stem (standing, broken, uprooted); (3) the remaining living length in metres along the main axis of the stem; (4) the remaining crown within the living length (%); (5) the illumination index (five levels, from least to most exposed to light); (6) the leaning of the trunk (in degrees); (7) defoliation within the remaining branches (%); (8) infestation by lianas in >

50% of the crown (presence/absence); (9) presence of stranglers on the trunk (presence/absence); (10) wounded trunk (three levels); (11) deformed trunk (three levels); (12) rotting trunk (three levels); (13) presence of fungi (presence/absence); and (14) obvious leaf damage (presence/absence). Trees found ‘broken’ and ‘uprooted’ were grouped into the ‘uprooted’ category. Except for survival status, all variables were collected in the field at the stem level. In seasonal forests, censuses were carried out during the wet season to distinguish between defoliation and deciduousness. Added to these 14 variables, we also considered the dbh measured in the previous full census of the plot and the topographic elevation of each tree.

The only two conditions that required post-fieldwork processing were the trunk loss and crown loss of each stem. We calculated trunk loss and crown loss relative to the ideal trunk and crown, respectively. The ‘ideal’ height of each trunk was estimated from a height–diameter model (eqn 6a in Chave *et al.*, 2014), re-scaled at each site to the known local maximum height. Then, the field estimates of remaining living lengths were compared with these ideal heights to estimate the relative trunk loss. To estimate the crown loss we used a model of the cumulative relative volume of tree trunk vs crown at a relative height  $r$  (Ver Planck & Macfarlane, 2014). We used this model to estimate the proportion of crown volume above and below a given height and multiplied it by the relative biomass of the crown ( $\frac{1}{3}$  of the total tree biomass; Chambers *et al.*, 2001; Duque *et al.*, 2017). Tree biomass was calculated based on the species wood density, the stem dbh and a site-specific environmental stress variable (Chave *et al.*, 2014; Réjou-Méchain *et al.*, 2017). Total crown biomass loss was calculated as ((estimated crown biomass above the remaining living length) + ((estimated crown biomass below the living length)  $\times$  (1 – estimated proportion of remaining crown within the living length))). Specific details on the calculation are provided in Methods S1.

### Assignment of mortality risk factors

We made no *a priori* assumptions regarding whether specific conditions represented mortality risk factors. Instead, we defined a condition as a mortality risk for a given species in a given site if the condition more than doubled the predicted probability of death in a fitted univariate model, that is, in a model in which the only fixed effect was the condition. We recognise that conditions are often confounded and that mortality depends on multiple conditions, but our dataset is not yet large enough to enable fitting multivariate models. Therefore, we constructed separate generalised linear mixed-effects models (GLMMs) for each site and condition to model the probability of death at the end of a given census interval as a function of the tree-level condition at the beginning of the interval. We used a logit link function and random intercepts and slopes depending on the species. GLMMs were fitted by maximum likelihood estimation (Laplace approximation) using the LME4 package in R (Bates *et al.*, 2015). In LME4 R notation, the formula was  $M \approx 1 + c + (1 + ds)$ , where  $M$  is the probability of mortality and  $c$  is the condition of each individual tree of species  $s$  at the beginning of a census interval. Each condition  $c$  was analysed separately (Table 1).

We fitted a model for each condition at each site, combining data across intervals. Each individual  $\times$  interval was treated as an independent observation in each site and, therefore, the estimated parameters give the mean effects over time periods, that is, without capturing temporal variation. We did not include random effects for census intervals because our dataset included only one to three census intervals per site, which was insufficient to characterise temporal variation and because our objective was to elucidate average species responses. The groups for which random intercepts and slopes were fitted were species with 10 or more individuals; species with less than 10 individuals were aggregated into larger taxonomic groups at the level of genera or families (Fig. S1). These groups are from this point forwards referred to as species. GLMM summary statistics and analyses of residuals (Hartig, 2021) are provided in Notes S1 and estimated coefficients for each condition and site are shown in Fig. S2.

The predicted probabilities from univariate GLMMs were used as a tool to assign mortality risks to individuals at the beginning of each interval. We first used the predictions from each site-level model to extract the species random slopes and determine which species were positively or negatively affected by each condition (Box 1). We disregarded negative slopes that lacked a plausible biological interpretation (e.g. higher survival under higher levels of crown loss). Second, for each condition  $c$  in each site, we defined ‘baseline’ mortality of each species ( $mq_{c,s}$ ) as the lowest modelled mortality probability among individuals of species  $s$ . Third, for each census interval  $t$  and type of condition  $c$ , we predicted the probability of death of each individual  $i$  of species  $s$  in each site ( $mp_{c,s,i,t}$ ). An individual tree was defined as ‘at risk’ if  $(mp_{c,s,i,t}/mq_{c,s}) > 2$ , that is if its probability of mortality was more than two-fold higher than the corresponding baseline mortality for its species in its site.

It is important emphasise that our analyses quantify *univariate associations* between individual conditions and mortality probability (controlling for species identity) and that these associations do not necessarily indicate causal relationships. Our univariate analyses inherently failed to control for other co-occurring conditions, which may be confounded. We initially attempted to perform Akaike information criterion (AIC)-based model selection for mortality models including all 15 conditions, their interactions and species random effects, but these models suffered from model overfitting and convergence issues. We did not explore multivariate models without species random effects because both the literature and our preliminary analyses indicated that species varied strongly in their responses to individual conditions. We considered a variable reduction approach, in which the conditions would be grouped into a few categories (e.g. physiological, environmental and mechanical). However, grouping factors *a priori* was largely arbitrary and conceptually flawed, because most of the conditions studied belonged to multiple groups. For example, the presence of lianas could be both a physiological factor (competition for light) or a disturbance/mechanical factor (heavy weight, lateral tensions). Alternatively, grouping conditions *a posteriori* based on patterns of co-occurrence resulted in groups without an intuitive or

**Table 1** Tree-level conditions ( $c$ , first column) evaluated at the beginning of the census intervals and how these were used (second column) to model and define mortality risk factors (third column) across six tropical forests.

Stem-level condition	Variable $c$ included in the GLMM $M \approx 1 + c + (1 + \text{cls})$	Tree-level mortality risk
1. Size	$c = \text{natural logarithm of diameter at the breast height (dbh)}$	1. Larger trees (+)
2. Elevation	$c = \text{elevation (standard normal deviates) within the plot}$	2. Smaller trees (-)
3. Illumination	$c = \text{illumination class}$	3. Higher elevations (+)
4. Physical state	$c = \text{categorical levels for the physical states of living trees: standing, broken and uprooted}$	4. Lower elevations (-)
5. Trunk loss	$c = \text{relative trunk loss}$	5. Light excess (+)
6. Crown loss	$c = \text{relative crown loss}$	6. Light limitation (-)
7. Defoliation	$c = \% \text{ of defoliation}$	7. Trunk broken (+)
8. Leaning	$c = \text{degrees of trunk leaning}$	8. Uprooted (+)
9. Fungal infection	$c = \text{presence of fungi}$	9. Trunk loss (+)
10. Leaf damage	$c = \text{presence of obvious leaf damage}$	10. Crown loss (+)
11. Liana(s) in crown	$c = \text{presence of } > 50\% \text{ liana load}$	11. Defoliation (+)
12. Strangler(s) on trunk	$c = \text{presence of stranglers on the trunk}$	12. Leaning (+)
13. Wounded trunk	$c = \text{size of wound}$	13. Fungal infection (+)
14. Deformities on trunk	$c = \text{size of deformity}$	14. Leaf damage (+)
15. Rotting trunk	$c = \text{size of rotting area}$	15. Liana(s) in crown (+)
		16. Strangler(s) on trunk (+)
		17. Wounded trunk (+)
		18. Deformities on trunk (+)
		19. Rotting trunk (+)

Generalised linear mixed-effects models (GLMM) were constructed to determine whether each condition was a species-specific mortality risk and assign risks to individual trees. As all variables, except elevation, were obtained at the stem level, conditions were estimated at the individual tree level as follows: maximum diameter at the point of measurement (dbh) across stems in the individual for the 'Size' condition; most representative physical state or mode across stems in the individual defined by basal area for the 'Physical state' condition; weighted value by the basal area of each stem in the individual for the 'Illumination index', 'Trunk loss', 'Crown loss', 'Defoliation', 'Leaning', 'Lianas', 'Stranglers', 'Wounded trunk', 'Deformities on trunk' and 'Rotting trunk' conditions; and the presence of the condition in any stem within the individual for the 'Fungal infection' and 'Leaf damage' conditions. The physical state of the tree was analysed as a categorical variable; the presence of 'Fungal infection' and 'Leaf damage' was analysed as binary variables; and the rest of the conditions was analysed as continuous variables. Symbols (+) and (-) in the third column indicate whether risk factors were defined from species with positive or negative slopes, respectively. Formula in the header of the second column refers to LME4 R notation to fit the univariate GLMMs, where  $M$  is the probability of mortality and  $c$  is the condition of each individual tree of species  $s$  at the beginning of a census interval.

mechanistic meaning, making inferences about risk factors even more complicated. After multiple preliminary analysis and much discussion, we abandoned these alternative approaches and focused on the definition of risk factors from univariate models. The results from univariate models are straightforward to interpret and can inform future experiments and multivariate modelling efforts.

### Prevalence, lethality and impact of mortality risk factors

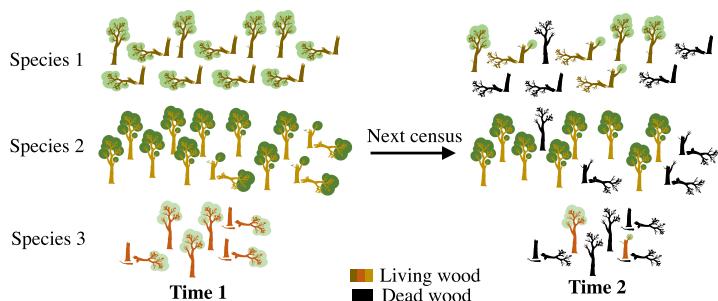
We calculated the prevalence, lethality and impact of each risk factor in each of the 14 census intervals (Box 1). We defined prevalence as the proportion of individuals in the forest with a given risk factor at the beginning of the interval. We defined lethality as the difference between the mortality rate of individuals *with* a given risk factor and the mortality rate of individuals *without* the risk factor, when controlling for species. Impact depends on prevalence and lethality; it was defined as the proportion of forest-wide mortality that is 'excess mortality' associated with the risk factor.

Due to the size- and habitat-stratified nature of our sample (Arellano *et al.*, 2021), our estimates could not be directly extrapolated from the sample to the whole forest. For example, small trees are under-represented in the sample compared with their

relative abundance in the forest. The same applies to species representation, with some common species possibly under-represented in our sample due to stratification by habitat. To infer patterns at the full 24–50 ha plot scale from our stratified sample, we assigned weights to each individual in the sample, so that under-represented types of individuals received greater weight than over-represented types of individuals. To do this, we classified all individuals in the forest and in the sample in discrete (size class  $\times$  taxonomic group) bins. Size class bins were based on the 35 dbh classes used in the sampling design (Arellano *et al.*, 2021), with limits exactly evenly distributed on a  $\log(\text{dbh})$  scale:  $\mathcal{E}^x, x \in \{\log_e(10) + 0z, \log_e(10) + 1z, \log_e(10) + 2z, \dots, \log_e(10) + 34z, \infty\}$  and  $z = (7 - \log_e(10))/34$ , in mm. If a (species  $\times$  size) bin present in the forest was absent from the sample, we assigned individuals in the forest to bins based on (genus  $\times$  size) or (family  $\times$  size) and/or the most similar size class. Finally, for each census interval, we assigned to each individual  $i$  in the sample a weight based on its bin equal to  $w_i = A/B$ , where  $A$  is the number of individuals in the forest in that bin and  $B$  the number of individuals in the sample in that bin. The overall distribution of weights in each site is provided in Fig. S3. These weights are interpreted as the number of trees in the full forest plot that each individual in the sample  $i$  represents and were used in all of the analyses to obtain forest-wide estimates. To provide

**Box 1** Definition of prevalence, lethality and impact of tree mortality risk factors. A worked example for the condition of physical damage (trunk broken).

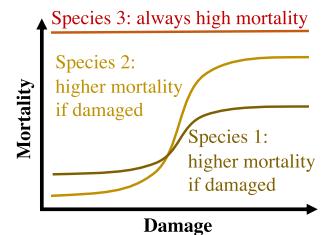
### (a) Field assessment



We first assess the damage condition of each tree at the beginning of a census interval (time 1) and the survival of each tree (coloured trees = alive; black trees = dead) at the end of the census interval (time 2). The relative frequency of each species ( $F_s$ ) is also recorded in time 1.

### (b) Risk definition

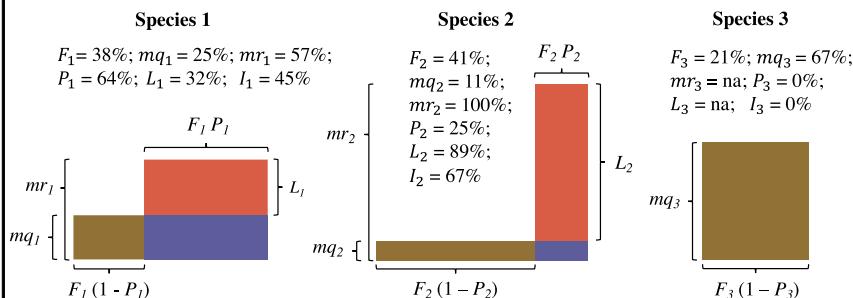
For each species, we evaluate how mortality rates relate to the damage condition and thereby determine whether damage constitutes a risk factor. Trees are defined as 'at risk' from a condition if they had the condition and that condition is associated with a mortality rate increase for their species to more than two times the baseline mortality (see the Materials and Methods section). In this example, damage is a risk factor for species 1 and 2, but not for species 3.



### (c) Species-level estimates

For each species  $s$ , we then calculate the prevalence, lethality and impact of the risk factor. The prevalence of the risk factor in species  $s$  ( $P_s$ ) is defined as the proportion of individuals of species  $s$  with the risk factor at the beginning of the interval. The lethality of the risk factor in species  $s$  ( $L_s$ ) is defined as the difference between the mortality rate of individuals *with* the risk factor ( $mr_s$ ) and the mortality rate of individuals *without* the risk factor ( $mq_s$ ). The impact of the risk factor on species  $s$  ( $I_s$ ) is defined as the proportion of mortality in the species that is 'excess mortality' associated with the risk factor.

$$L_s = mr_s - mq_s; \quad I_s = \frac{mr_s}{(F_s P_s + mr_s)} = \frac{P_s L_s}{(mq_s + P_s L_s)}$$



These rectangles show how total mortality in each species is divided among mortality in trees without the risk factor (brown), baseline mortality in trees with the risk factor (blue) and excess mortality in trees with the risk factor (red). na, not applicable.

The widths of the rectangles indicate the number of trees of the respective species *without* (brown) and *with* (blue and red) the risk factor in time 1 and the heights indicate the mortality rates; therefore, the areas are proportional to the number of dead individuals in each group. The impact is therefore calculated as the excess mortality in trees with the risk factor (red area) as a proportion of the total mortality of the species (the sum of green, blue and red areas).

### (d) Stand-level estimates

We finally calculate stand-level prevalence, lethality and impact. The prevalence of the risk in the stand ( $P_{\text{stand}}$ ) is the proportion of all trees in the forest with the risk factor. The lethality of the risk in the stand ( $L_{\text{stand}}$ ) is the average increase in mortality of trees with the risk factor over conspecifics without the risk factor. The impact of the risk in the stand ( $I_{\text{stand}}$ ) is the proportion of total mortality in the forest that is excess mortality associated with the risk factor (the sum of all red areas divided by the sum of all coloured areas in (c)).

$$P_{\text{stand}} = \sum F_s P_s = 35%; \quad L_{\text{stand}} = \frac{\sum F_s P_s L_s}{\sum F_s P_s} = 49%; \quad I_{\text{stand}} = \frac{\sum F_s P_s (mr_s - mq_s)}{\sum (F_s mq_s + P_{\text{stand}} L_{\text{stand}})} = \frac{\sum F_s P_s (mr_s - mq_s)}{\sum (F_s mq_s + P_{\text{stand}} L_{\text{stand}})} = 38%$$

context for our estimates of mortality rates with and without risk factors, we calculated mean mortality rates for each forest and census interval using sample bins as ‘subpopulations’ (eqn 8 in Sheil & May, 1996) (Methods S2).

Given that species varied in the prevalence and lethality of risk factors and that risk factors are defined based on species groups in the GLMMs, we accounted for the among-species heterogeneity in calculating the overall lethality and the impact of each risk factor (Box 1). We first defined  $S$  as the set of individuals in the sample that belong to the species  $s$ ;  $D$  as the set of individuals in the sample that were found dead at the end of the interval;  $R$  as the set of individuals in the sample with the risk factor at the beginning of the interval;  $Q$  as the set of individuals in the sample without the risk factor at the beginning of the interval; and  $T$  as the mean census interval length in years. For each census interval and site, we calculated the frequency of species  $s$  in the forest ( $F_s$ ), the prevalence of each risk factor in species  $s$  ( $P_s$ ), the annual mortality rate of trees with the risk factor in species  $s$  ( $mr_s$ ) (Kohyama *et al.*, 2018), the annual mortality rate of trees without the risk factor in species  $s$  ( $mq_s$ ) and the lethality of each risk factor in species  $s$  ( $L_s$ ), as follows:

$$F_s = \sum_{i \in S} w_i$$

$$P_s = \frac{\sum_{i \in [S \cap R]} w_i}{\sum_{i \in S} w_i}$$

$$mr_s = 1 - \left( 1 - \frac{\sum_{i \in [S \cap R \cap D]} w_i}{\sum_{i \in [S \cap R]} w_i} \right)^{(1/T)}$$

$$mq_s = 1 - \left( 1 - \frac{\sum_{i \in [S \cap Q \cap D]} w_i}{\sum_{i \in [S \cap Q]} w_i} \right)^{(1/T)}$$

$$L_s = mr_s - mq_s$$

We then calculated stand-level prevalence ( $P_{\text{stand}}$ ), stand-level lethality ( $L_{\text{stand}}$ ) and stand-level impact ( $I_{\text{stand}}$ ), as:

$$P_{\text{stand}} = \sum F_s P_s$$

$$L_{\text{stand}} = \frac{\sum F_s P_s L_s}{\sum F_s P_s}$$

$$I_{\text{stand}} = \frac{P_{\text{stand}} L_{\text{stand}}}{\sum (F_s mq_s) + P_{\text{stand}} L_{\text{stand}}}$$

A worked example of these calculations for the damage condition of trunk broken is shown in Box 1.

We calculated prevalence, lethality and impact for each site  $\times$  interval and reported their means and standard deviations. These standard deviations provide a simple first estimate of variability among sites and over time; they do not represent an accounting of the overall uncertainty related to observational error and process variability. We acknowledge that there are many sources of error and uncertainty in our estimates (i.e. field measurements,

allometric models, uncertainty in parameter estimation and the conversion to forest-wide estimates). A full accounting and propagation of these errors is beyond the scope of the current work.

We evaluated the robustness of our results to details of our methods and the generality of results across individual sites. Our main analyses upscale our results to all trees  $\geq 10$  mm dbh in the forest using weights; we also report results just for our observed sample and when upscaling only trees  $\geq 100$  mm dbh. We also reported the main results based on arbitrary definitions of ‘risky conditions’ in the sample, that is not model-informed risk factor assignments. Examples of arbitrary definitions of ‘risky conditions’ include the assignment of: a ‘Crown loss’ risk to trees with  $> 10\%$  loss in the crown; a ‘Defoliation’ risk to trees with  $> 10\%$  defoliation; etc. Our main analyses define species groups for the GLMM random effects using at least 10 individuals; we fitted models and reproduced the main results for groups with at least 5 and 30 individuals. Our main analyses define a condition as a risk factor if it elevates mortality rates two-fold within taxonomic groups; we repeated the analyses using 1.5-fold and 3-fold thresholds instead. Finally, we also reported results for individual sites, combining census intervals within sites.

### Co-occurrence of mortality risk factors

We evaluated the role of multiple risk factors in contributing to mortality by grouping trees by the number of risk factors and then calculating annual mortality rates for each group (using the same formula applied previously for taxonomic groups and risk factors), together with the upscaled proportion of all trees and of dead trees contributed by each group. We evaluated co-occurrence among pairs of risk factors by quantifying the proportion of trees with a given risk factor that were assigned each other risk factor.

### Association of conditions and risk factors with modes of death

To assess whether dead trees assigned different modes of death (i.e. standing, broken, uprooted or undetermined) differed in the distributions of prior conditions and mortality risk factors, we conducted tests on the combined data from all intervals and sites (sample sizes within individual sites and census intervals were low, limiting statistical power for site-specific analyses). For continuous variables (i.e. tree size, elevation, trunk/crown damage, defoliation and leaning), we tested for differences in distributions among groups using global Kruskal–Wallis tests (nonnormally distributed ANOVA residuals, Kolmogorov–Smirnov test,  $P < 0.05$ ) and then conducted pairwise Wilcoxon rank sum tests. For categorical variables (including risk factors), we tested for differences in proportions among groups using chi-squared tests.

All analyses were performed in R v.4.0.4 (R Core Team, 2021).

## Results

The trees we evaluated spanned all topographic positions, light environments and sizes  $\geq 10$  mm dbh within each forest (Figs 1,

S4). Most of the trees were standing and upright. Except for being light limited, most of them had no evidence of conditions expected to negatively affect survival (Fig. 1). We recorded 2100 tree deaths among our 99 858 observations (tree  $\times$  census interval) in 14 one-year census intervals. Upscaling by size class and taxonomic group, this corresponded to average annual forest-wide mortality rates of  $2.2\% \text{ yr}^{-1}$  ( $1\text{SE} = 0.2\% \text{ yr}^{-1}$ ) for trees  $\geq 100 \text{ mm dbh}$  and  $3.9\% \text{ yr}^{-1}$  ( $1\text{SE} = 0.4\% \text{ yr}^{-1}$ ) for all trees  $\geq 10 \text{ mm dbh}$  (Table S1).

Mortality risk factors varied in their prevalence, lethality and impact (Fig. 2). Light limitation was the most assigned risk factor (recorded in an average of 72% of trees in a site  $\times$  interval), followed by small-tree risk (27%) and damage-related risks: crown loss, trunk loss and trunk broken (13–20%; Fig. 2a). These highly prevalent risk factors exhibited relatively low lethality ( $3\text{--}11\% \text{ yr}^{-1}$ ; Fig. 2b) but were the most impactful in terms of their contribution to total mortality: 53% for light limitation and 22–45% for damage-related risk factors (Fig. 2c). The most lethal risk factor was leaf damage, which was associated with an increase in mortality rate of 60% per year (that is, a tree that would have had a mortality rate of 3% without leaf damage would have a mortality rate of 63% with leaf damage), followed by wounds, rotting and uprooting (lethality of 19–23% per year; Fig. 2b). However, these highly lethal risks had relatively low impact (< 3.1% of mortality), reflecting their low prevalence (< 2.5% of trees). Leaning, defoliation and lower elevation risks were moderately impactful risk factors, each contributing more than 4.5% of total mortality; these were each present in over 4.6% of trees (prevalence) and exhibited lethaliites of 5–14%. Across risk factors, there was a significant correlation between impact and prevalence (Pearson's correlation ( $r$ ) = 0.86,  $P < 0.001$ ) but no relationship between impact and lethality ( $r = -0.29$ ;  $P > 0.05$ ) or between lethality and prevalence ( $r = -0.30$ ;  $P > 0.05$ ).

The ranking of importance of risk factors was generally maintained when weights were not used to upscale to the forest level (i.e. estimates from the sample; Fig. S5), when '*risky conditions*' were defined in a discretionary way instead of being model-informed risks (Fig. S6), when analyses were performed separately for each site (Fig. S7), when only large trees ( $\geq 100 \text{ mm dbh}$ ) were analysed (Fig. S8), when other thresholds were used in the risk definition (Figs S9–S11), or when mortality models used to define risks used different minimum taxonomic group sizes (Fig. S12).

Overall, we found that 82% of all living trees had at least one risk factor, with 44% of these trees having only one risk and the others having between two and nine risk factors (Fig. 3a). The estimated forest-wide mortality rate for trees without risk factors was  $2.2\% \text{ yr}^{-1}$  ( $1\text{SE} = 0.6\% \text{ yr}^{-1}$ ), compared with  $5.1\% \text{ yr}^{-1}$  ( $1\text{SE} = 0.7\% \text{ yr}^{-1}$ ) for trees with one or more risks. Mortality rates increased with the number of assigned risks, from  $2\% \text{ yr}^{-1}$  for trees with one risk to  $33\% \text{ yr}^{-1}$  for trees with nine risks (Fig. 3b). The 82% of trees with one or more risk factors accounted for 91% of the overall mortality (or  $3.6\% \text{ yr}^{-1}$  forest-wide mortality), whereas the 18% of trees with no assigned mortality risks accounted for 9% of the overall mortality (or  $0.3\% \text{ yr}^{-1}$  forest-wide mortality; Fig. 3c). Eighty-seven percent of the dead trees in the forests were trees that had had between one and five risks at

the beginning of the interval (Fig. 3c). Co-occurrence of pairs of risk factors largely followed expectations based on the prevalence of individual risk factors, but there were some risks that were disproportionately more likely to co-occur (e.g. combinations of the damage-related risks) (Fig. 4).

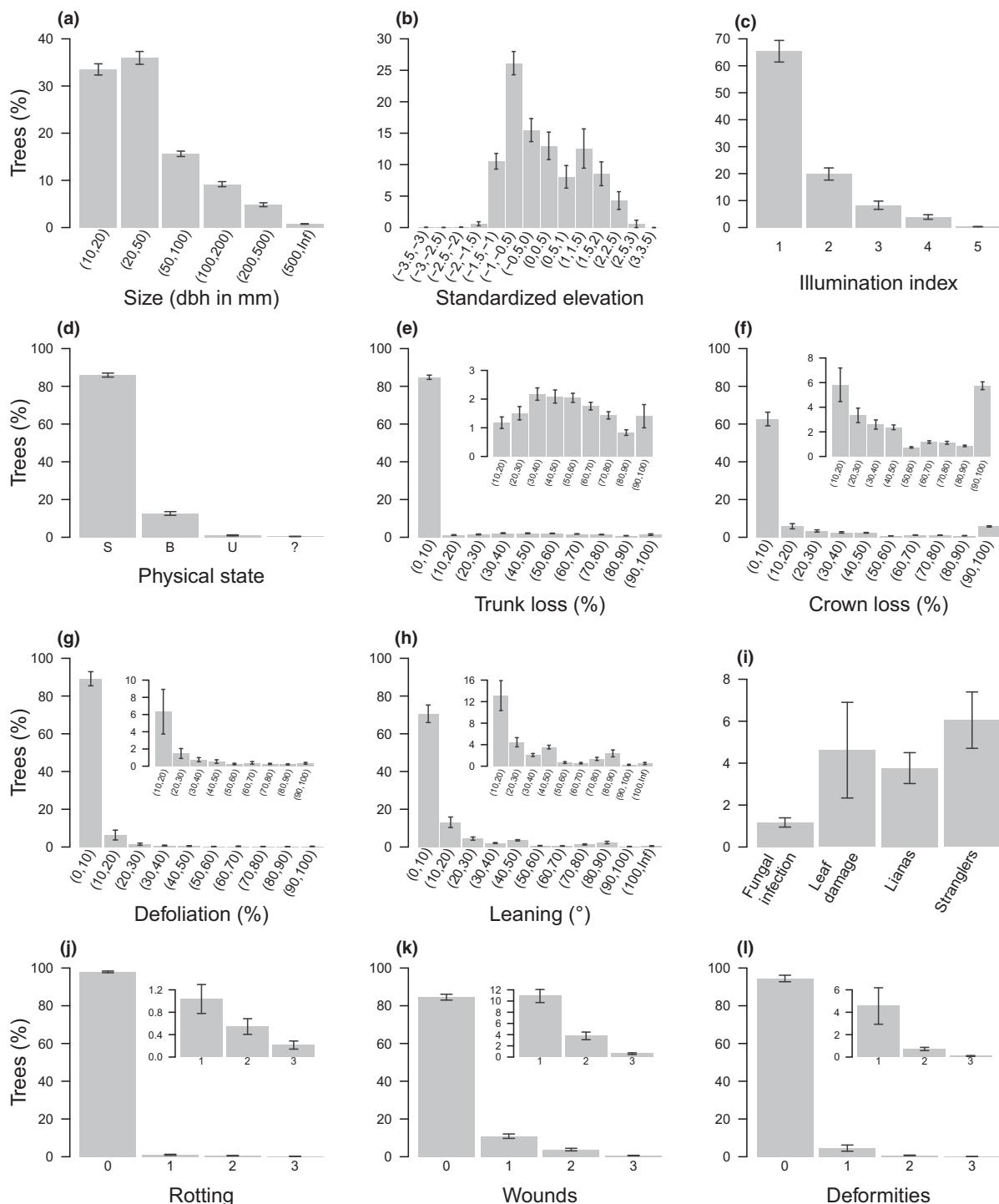
There was very limited systematic variation in conditions across the modes of death and in risk factors across the modes of death (Figs 5, 6) mainly due to the high level of co-occurrence of risk factors in any given mode (Figs 4, 6). Of the 2100 trees found dead across the 14 intervals, 36%, 28%, 11% and 25% were found standing, broken, uprooted and with an unidentified mode, respectively. For the 15% of dead trees (308) that were not assigned any risk factors while still alive, 37%, 29%, 11% and 22% died standing, broken, uprooted and with an unidentified mode of death, respectively (Fig. 6b). Dead uprooted trees had the most different conditions and risk factors while alive: they were significantly larger, tended to be located at lower elevations, had lower values of trunk and crown damage and were more leaning than dead standing and dead broken trees. Dead broken and standing trees were not different in their size or elevational location; but dead broken trees had significantly higher trunk and crown damage than standing and uprooted trees (Fig. 5). Consequently, the proportion of dead trees that were assigned the trunk/crown loss risk factors was higher for dead broken than for dead standing or uprooted trees (Fig. 6). Differences in illumination values, the presence of fungal infections and wounds, as well as their associated risk factors across the modes of death, were mainly driven by trees with unidentified modes (Fig. 5), which were mostly composed by small, light-limited trees and had the lowest incidence of fungal infections and wounds conditions (Fig. 6).

## Discussion

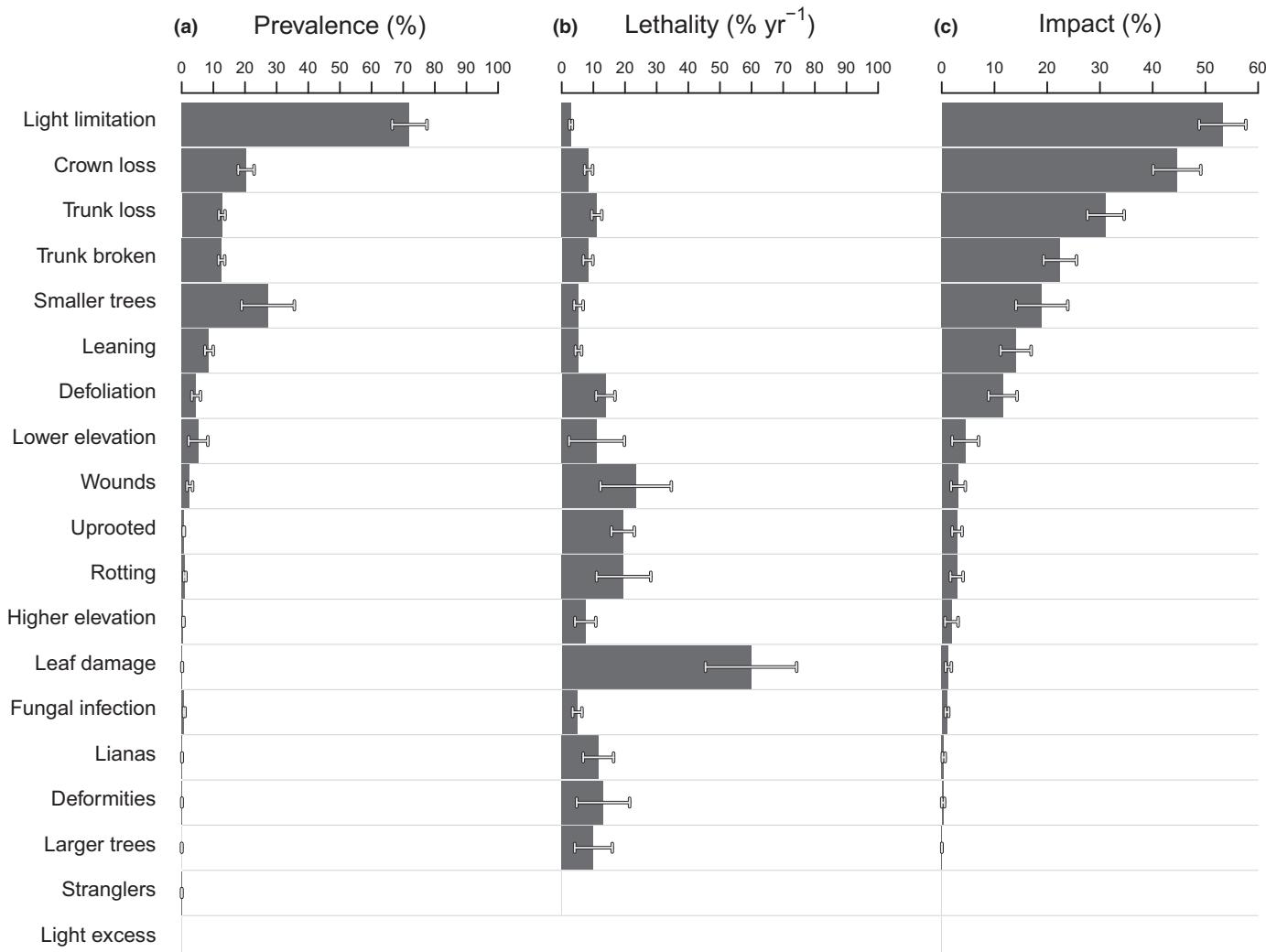
### Relative importance of tree-level mortality risk factors

The most important mortality risk factors, by impact, were those related to crown/trunk loss, light limitation and small size. Leaning, defoliation and lower elevation ranked next in impact, whereas other risks expected to be important such as those associated with lianas, stranglers, trunk deformities and trunk rot were not prevalent or impactful in this study. This ranking should inform research priorities and model experiments to improve predictions of the fate of forests in global dynamic vegetation models (McDowell, 2018; Longo *et al.*, 2019; Pugh *et al.*, 2020). For example, the measurement of the physiological consequences, that is, carbon starvation and hydraulic failure, across trees with different levels of damage can help to predict the biomass consequences of specific disturbance types in tropical forests.

Conditions associated with resource availability (light limitation, small-tree size and, to a lesser extent, topographic position) played an important role among the risk factors studied. Light is an important limiting factor related to tree death (Hubbell *et al.*, 1999; Wright *et al.*, 2015). Light-limited trees, which are mostly small (Fig. 4), are expected to die more by competition than large and fully exposed trees (Coomes *et al.*, 2003; Muller-Landau *et al.*, 2006). They also have lower photosynthetic rates that may



**Fig. 1** Estimated forest-wide frequencies of tree-level conditions on living trees, with means (bars) and SE (whiskers) calculated over 14 sites by census interval combinations (from six tropical forest sites). Panels (a–h) show the distribution of trees in the forests across size (a), elevation (b), illumination (c), physical state (d), trunk loss (e), crown loss (f), defoliation (g), and leaning (h) classes. In (b), values refer to the standard normal deviations of the elevation within the plot. In (d), 'S' refers to standing; 'B' to broken, 'U' to uprooted, and '?' to unidentified physical states in living trees. Trees found 'B' and 'U' were grouped into the 'U' category. The 'Unidentified' physical state refers to cases in which the field crews were uncertain. Panel (i) shows the percentage of trees in the forests with fungal infection, leaf damage, lianas in the crown and stranglers on the trunk. Panels (j–l) show the percentage of trees with different levels of rotting (j), wounds (k), and deformities on trunk (l). In (j–l), '0' refers to absence, '1' to small, '2' to large and '3' to massive. Inset figures show the distribution of a given condition from the second class (i.e. removing the first, most common class) and are presented to improve visualisation of condition distributions. All values are based on extrapolating from the observed sample to all trees  $\geq 10$  mm diameter at the point of measurement (dbh) in the forest as a whole, with extrapolation based on weighting factors accounting for differences in abundances across classes defined by combinations of dbh and taxonomic group. Tree-level conditions in the sample (i.e. not upscaled to the forest level) are provided in Supporting Information Fig. S4.

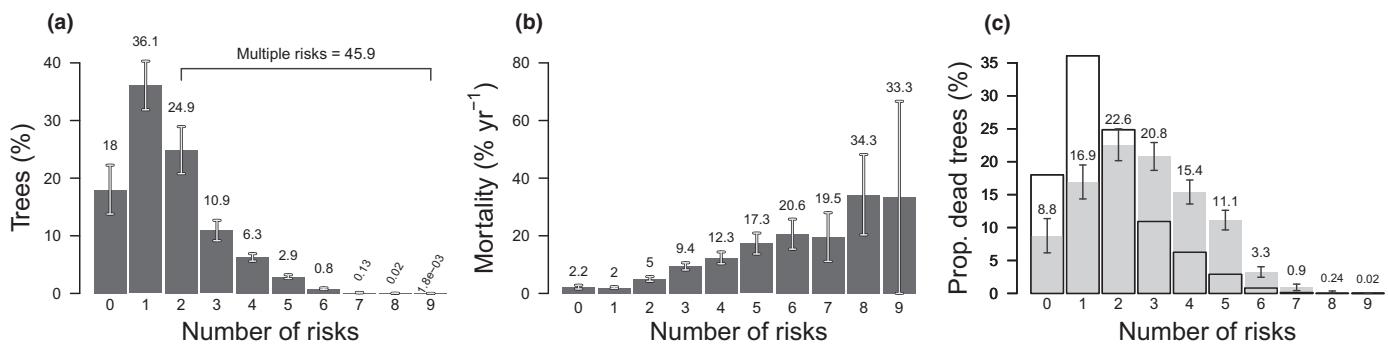


**Fig. 2** Estimated forest-wide prevalence, mortality and impact of 19 risk factors assessed during 14 one-year census intervals in six tropical forests. Prevalence (a) is the estimated proportion of individuals in the forest with the risk factor at the beginning of the interval. The lethality (b) is the difference between the mortality rate of individuals *with* a given risk factor and the mortality rate of individuals *without* the risk factor. The impact (c) is the proportion of total mortality in the forest that is ‘excess mortality’ associated with the risk factor, that is, the estimated percentage of mortality that would not have occurred if the risk factor is not present in the forest. Note that having a risk factor means that the tree both had the condition and was estimated to have a mortality rate elevated more than two-fold compared with baseline because of it. Risk factors are ranked by impact. Error bars are SE estimated from the 14 sites by census interval combinations among the six sites. All values are based on extrapolating from the observed sample to all trees  $\geq 10$  mm diameter at the point of measurement (dbh) in the forest as a whole, with extrapolation based on weighting factors accounting for differences in abundances across classes defined by combinations of dbh and taxonomic group. Estimates based on the sample (i.e. not upscaled to the forest level) are provided in Supporting Information Fig. S5. Estimates based on arbitrary definitions of ‘risky conditions’ in the sample, not model-informed risk factor assignments, are provided in Fig. S6. Estimates for each site, for large trees ( $\geq 100$  mm dbh) and using other thresholds in the definition of risks are presented in Figs S7–S10.

lead to death following the depletion of nonstructural carbohydrates (Kobe, 1997; Poorter & Kitajima, 2007) and are more likely to be impacted by falling branches and neighbouring trees (Fig. 4). Because our analyses were weighted to be representative of all trees with dbh  $\geq 1$  cm, most trees were light limited and this risk factor had the highest prevalence as well as the highest impact (Fig. 2). Even when restricting analyses to trees with dbh  $\geq 10$  cm, light limitation still had the highest prevalence and the second-highest impact (Fig. S8). However, it is important to clarify that the frequency of a condition in the forest and the impact of the associated risk factor are not necessarily correlated, as this

relationship is mediated by both the species-level sensitivities to the conditions and the lethality of the risk when it is present (Box 1).

Being at lower elevations than the average for a given species was associated with a higher risk of mortality than being at higher elevations. Variation in below-ground resources, in contrast with light limitation, is largely determined by topography and leads to variation in individual-level performance among topographically defined habitats (Bunyavejchewin *et al.*, 2019; Zuleta *et al.*, 2020). Although lower elevation locations or valleys are generally wetter than slopes or ridges, trees in valleys face flooding more frequently (Margrove *et al.*, 2015; Moser *et al.*, 2019) and are



**Fig. 3** Estimated forest-wide proportion of trees, mortality and percentage of total mortality for trees with zero to nine risk factors across 14 sites by census interval combinations in six tropical forest sites. Values in (a) show the proportion of individuals in the forest with a given number of risk factors (including no risks, 0) at the beginning of the interval. Mortality (b) is the proportion of individuals that died during the census interval among those that started the interval with a given number of risk factors. The percentage of total mortality (c) is the proportion of dead individuals in the forest that had a given number of risk factors at the beginning of the interval (grey bars). For reference, empty bars in (c) show the proportion of trees with the risk. Error bars are SE estimated from the 14 census intervals among the six sites. Numbers above bars indicate the exact percentage. All values are based on extrapolating from the observed sample to all trees  $\geq 10$  mm diameter at the point of measurement (dbh) in the forest as a whole, with extrapolation based on weighting factors accounting for differences in abundances across classes defined by dbh and taxonomic group.

sensitive to extreme water shortage because they tend to prioritise efficient water transport over hydraulic safety (Cosme *et al.*, 2017; Zuleta *et al.*, 2017). That said, topographic-related risks were particularly variable across sites (see later; Fig. S7).

Trees with crown or trunk damage in the previous census had an impact on forest mortality of 22–45%. The importance of these risks results from both their high prevalence (13–20%) and moderate lethality (8–11%). Damaged trees are more prone to die because of the loss of photosynthetic capacity, large energetic costs of repair (Anderegg *et al.*, 2012; Trugman *et al.*, 2018; Arellano *et al.*, 2019) and increased exposure to pathogens and pests (Dyer *et al.*, 2012). Trunk and crown damage may result from mechanical stress (e.g. wind, storms, branch fall, treefall, lightning, etc.) or the decay of standing trees due to physiological stress (e.g. resource limitation, drought, herbivory, etc.), or some combination of both. Observational studies such as this one cannot disentangle losses due to physiological vs mechanical causes. The relatively moderate lethality of damage-related risks compared with other risks such as leaf damage, fungal infections or defoliation indicates that an important proportion of damaged trees can survive from year to year. Indeed, trees are capable of recovering following structural or physiological damage (Ruslandi & Putz, 2012; Anderegg *et al.*, 2015; Shenkin *et al.*, 2015; Magnabosco Marra *et al.*, 2018; Kannenberg *et al.*, 2020). As modular organisms, trees can delay death or recover by compartmentalising damage (Shigo, 1984; Finch, 1990; Bernard *et al.*, 2020). This trait, along with the ability to resprout, constitute key traits that allow trees to withstand damage (Putz & Brokaw, 1989; Paciorek *et al.*, 2000; Su *et al.*, 2020).

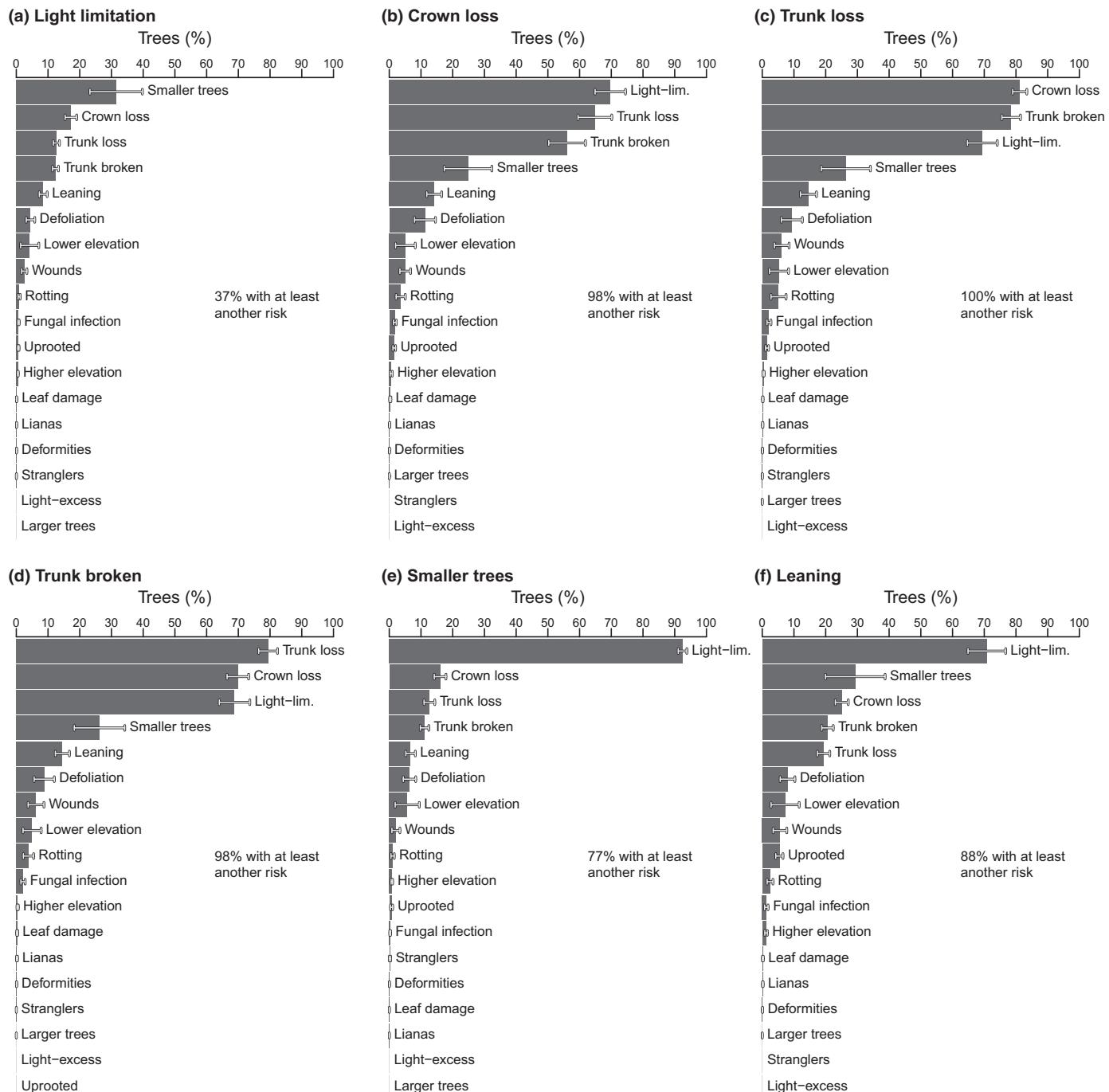
After risks related to resource limitation and wood damage, leaning and defoliation were the next most important risk factors experienced by trees. A leaning trunk is more vulnerable to breakage and/or uprooting (Fig. 4) and can imply suboptimal allocation, given that more wood is required for the same absolute height growth (Fournier *et al.*, 2006; Bragg & Shelton, 2010; Shenkin *et al.*, 2015). Given the relatively high prevalence of this risk factor, studies that remove leaning trees to estimate

demographic rates are likely to be biased towards healthier-than-average trees (e.g. Lieberman *et al.*, 1985; Visser *et al.*, 2016). Defoliation, conversely, was rarely recorded in the field (Fig. 1g), but the high lethality associated with this condition resulted in a moderate impact. The role of defoliation on mortality has been widely shown in temperate forests (Dobbertin, 2005); here we provide the first evidence for its importance in tropical forests. Although death in a defoliated tree may have resulted from reduced photosynthesis and induced carbon starvation, defoliation can also be a symptom or consequence of other mechanisms killing a tree (Fig. 4).

Although the forests included in this study differed in composition and environmental conditions, the relative importance of the main risk factors were similar (Fig. S7; also evidenced from the error bars in Fig. 2). Even the estimated coefficients in the mortality models used to assign these risks reflected consistent effects across sites (Fig. S2). Risks related to topographic conditions and size (and their associated models) were the most variable among sites. ‘Lower elevation’ was assigned as a risk factor only in Amacayacu (Colombia), HKK (Thailand) and Pasoh (Malaysia); while the ‘smaller tree’ risk was more important in HKK and KC (Thailand), and in Fushan (Taiwan). These differences may be a consequence of the different local impact of El Niño related droughts in 2015–2016, which are expected to leave a topography and tree size signature (Zuleta *et al.*, 2017; Gora & Esquivel-Muelbert, 2021). Unfortunately, our time series was not enough to study the relationship between climate and mortality patterns. The continued monitoring of conditions of living trees and their fate under ongoing climatic changes will enable the assessment of climate-related mortality risks and their multivariate interactions with the tree-individual mortality risk factors studied here.

#### The limited inference from modes of death

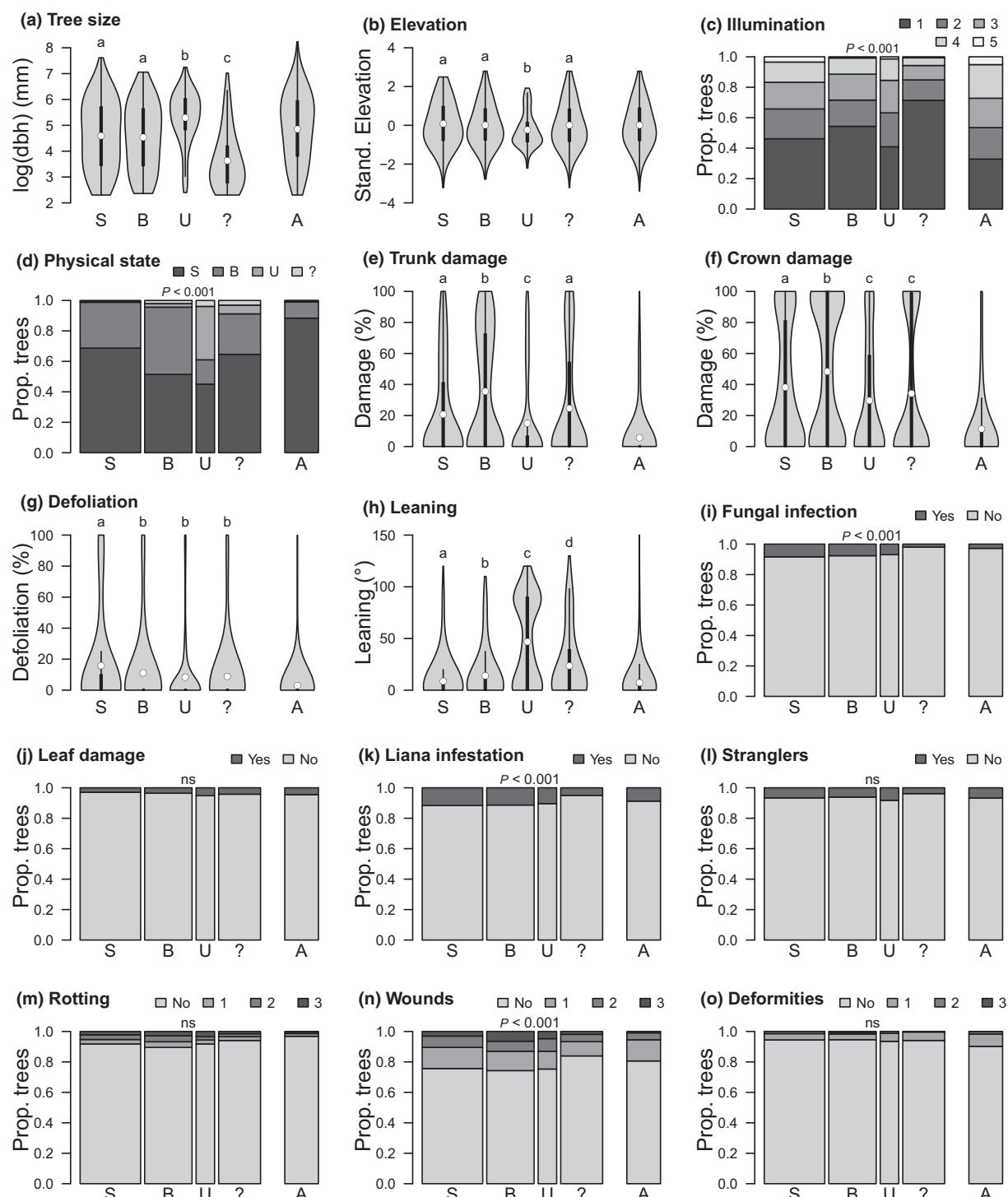
*Post mortem* designation of modes of death has been the standard method for inferring mortality mechanisms in observational



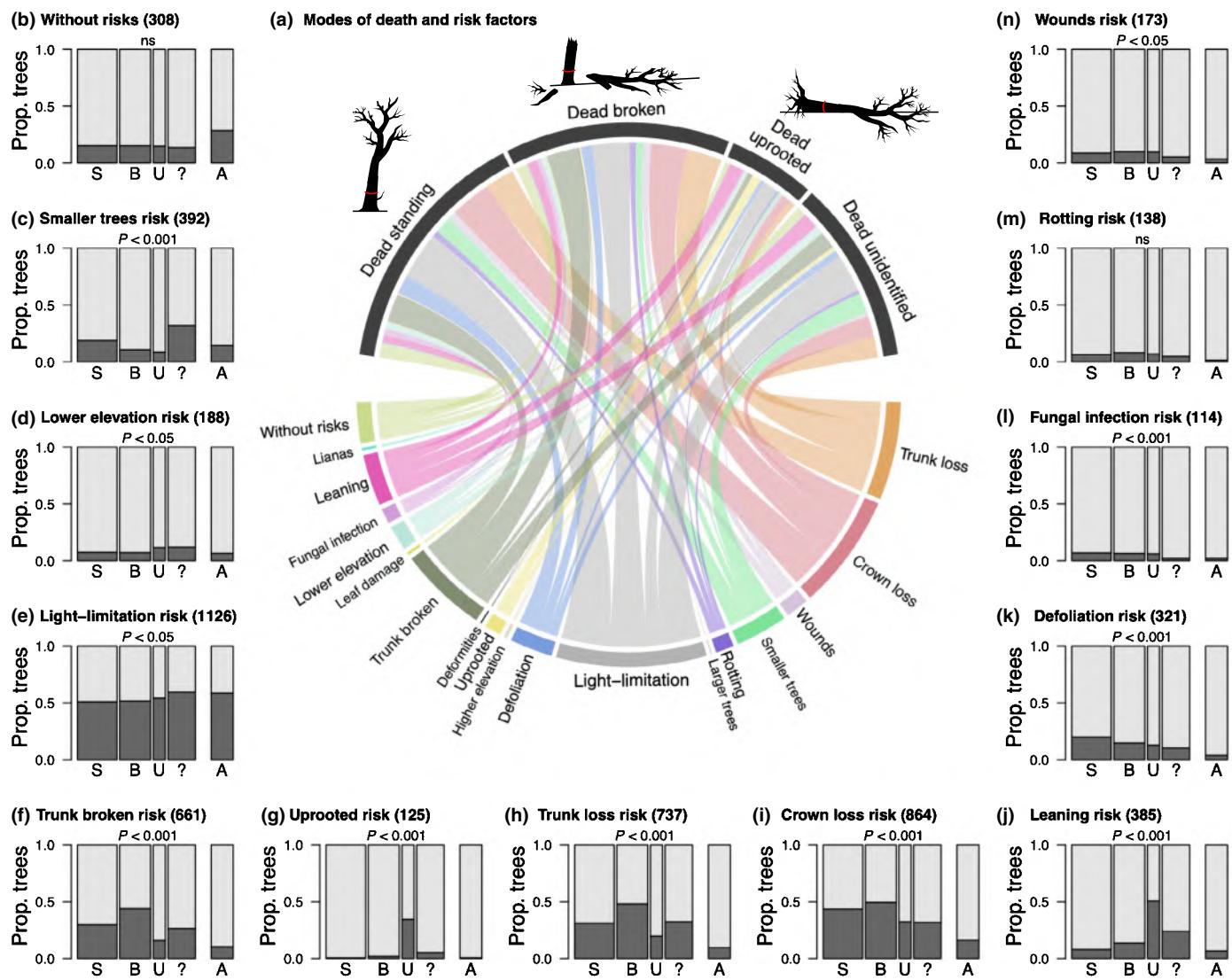
**Fig. 4** Co-occurrence of risk factors for each of the six most impactful risks: light limitation (a), crown loss (b), trunk loss (c), trunk broken (d), smaller trees (e) and leaning (f). For each risk factor, bars in each panel show the percentage of trees with the risk factor that were also assigned other risks. Error bars are SE estimated from the 14 sites by census interval combinations among the six sites. Co-occurrence for the rest of the risks and specifically among dead trees (commonly referred to as multimorbidity) are provided in Supporting Information Figs S13 and S14, respectively.

studies, where dead standing and dead broken/uprooted have been attributed to physiological and mechanical causes of death, respectively (Gale & Barfod, 1999; Slik, 2004; Chao *et al.*, 2009; De Toledo *et al.*, 2011). Using this approach, for example, half of the deaths in neotropical forests were recently attributed to mechanical damage caused by winds or storms and the other half to physiological mechanisms such as competition for resources or drought stress (Esquivel-Muelbert *et al.*, 2020). Our analyses of

the relationship between the modes of death and the conditions and risk factors of the same trees before they died suggest very limited evidence for the assumptions implicit in the *post mortem* approach. For example, we may have expected light-limited trees to die mostly standing, but the proportion of dead trees with low values of illumination index was higher among broken than standing dead trees (Fig. 5c). These results are largely driven by the high levels of co-occurrence among risk factors (Figs 4, 6).



**Fig. 5** Frequencies of tree-level conditions of living trees that were subsequently (in the next census) found dead standing (S), broken (B), uprooted (U), or with an unidentified (?) mode of death in six tropical forests. The ‘Unidentified’ mode of death refers to trees for which only the tag was found because they fully decomposed or were beneath fallen trees in a gap. Different letters above bars indicate significant differences in the conditions among the modes of death for continuous variables (a, b, e–h; Wilcoxon rank sum after Kruskal–Wallis tests) and differences in the proportion of dead trees in each group for categorical and binary variables (c, d, i–o; chi-squared tests). ns, nonsignificant differences. Conditions of surviving trees ('A' for Alive) are also shown for reference but not tested for differences. In the legend of (d), 'S' refers to standing; 'B' to broken, 'U' to uprooted, and '?' to unidentified physical states in living trees. The ‘Unidentified’ physical state in living trees refers to cases in which the field crews were uncertain. Violin plots in (a, b, e–h) show the distribution of measured values within each mode of death: white circles indicate the mean and the shape as a whole indicates the full distribution of values. Violin plots are truncated according to the range of the variable: at zero for (a, e–h) and at 100% for (e–g). In categorical and binary variables (c, d, i–o), the width of each bar is scaled to the proportion of the population in the given category (36% dead standing, 28% broken, 11% uprooted and 25% unidentified, respectively).



**Fig. 6** Frequencies of given mortality risk factors assigned based on previous conditions among trees subsequently found dead standing (S), broken (B), uprooted (U), or in an unidentified (?) mode of death in six tropical forests. The 'Unidentified' mode of death refers to trees for which only the tag was found because they fully decomposed or were beneath fallen trees in a gap. Chord diagram in (a) shows the association between modes of death and risk factors. The lower half of the circle corresponds to the 2100 dead trees without risks or with each of the 19 risk factors, while the upper half-section indicates their modes of death after 1 yr. The arc of the circle in the upper half-section corresponds to the proportion of trees found dead standing, broken, uprooted and with an unidentified mode of death. Colours of the links indicate different risk factors and the width of the link (chord) is proportional to the number of trees. Specific proportions across modes of death are shown in (b–n) for trees without risks (b) and for risk factors with at least 50 dead trees (c–n). Dark grey and light-grey colours of the bars correspond to trees with or without the given risk, respectively. P-values above the bars indicate significant differences among modes of death (chi-squared tests). ns, nonsignificant differences. The width of each bar is scaled to the proportion of the population in the given category (36% dead standing, 28% broken, 11% uprooted and 25% unidentified, respectively). Numbers in parentheses in (b–n) show the total dead trees with the given risk.

Even in cases in which statistically significant differences in the conditions were found across modes of death (e.g. dead uprooted trees had higher values of leaning before dying and dead broken trees had higher trunk and crown damage before dying), trees found dead with a specific mode share many pre-death conditions and risk factors that often result from a mix of mechanical and physiological stressors (Fig. 6; Franklin *et al.*, 1987; Das *et al.*, 2016). Substantial proportions of dead trees found broken and uprooted have been reported with pre-existing fungal infections and/or wood rotting in temperate forests (Larson & Franklin, 2010, and references therein). The limited inference from modes of death is reinforced

in tropical forests, where the high rates of wood decomposition quickly remove signs of the killing agent (Wieder *et al.*, 2009; Gora *et al.*, 2019) and the interval between forest censuses is typically long and highly variable (e.g. Davies *et al.*, 2021; ForestPlots.net *et al.*, 2021). We therefore urge caution in the inference of tree mortality mechanisms using *post mortem* surveys.

#### Predicting short-term tropical tree mortality

Here, 91% of trees that died in these forests had at least one risk factor 1 yr before being found dead. These results suggest that,

typically, tree death is not an immediate event due to unpredictable episodic disturbances, but the result of chronic or lagged mechanisms that take some time to develop and kill the tree (Espírito-Santo *et al.*, 2014; Fontes *et al.*, 2018; Arellano *et al.*, 2019; Griffiths *et al.*, 2021). If death is slow and deterministic, rather than sudden and stochastic, then it may be predictable at the individual level. Individual-level mortality models could better represent mortality rates by including the most important processes linked to the tree-level conditions studied here.

Some of the tree deaths happened with no prior risks on the tree. These may be cases in which lightning, storms, landslides or other events abruptly kill trees within the one-year census period (Dykes, 2002; Negrón-Juárez *et al.*, 2010; Margrove *et al.*, 2015; Vincent *et al.*, 2018). Other deaths may reflect senescence attributed to age alone (Chao *et al.*, 2009; De Toledo *et al.*, 2011), but evidence of genetically programmed senescence is very limited in perennial plants (Munné-Bosch, 2008; Piovesan & Biondi, 2020) and we expect any senescence-related risks to be at least partially captured by our 'larger trees' risk factor. In other cases, our methods may have failed to assign relevant risk factors to these trees. Some of the trees that died with no assigned risk factors may have been unhealthy the year before as noted in our condition scores, but the associated increase in the assigned probability of death may not have been sufficient to trigger a label of risk factor in our analysis. These numbers are obviously dependent on the threshold used to define risks; by definition, the higher the threshold, the higher the number of trees that will die without mortality risk factors. Finally, we focused on easily observed environmental and physical attributes of the trees to assess risk factors. We expect some fraction of the trees to die due to diseases, pathogens or other physiological stressors for which there was no external manifestation. More informative functional and physiological traits could probably improve the predictive power of mortality models.

## Conclusions

We provide the first ranking of importance of tree-level mortality risk factors in tropical forests. In addition to factors related to resource limitation (proxied by illumination, size and topography), tree-level damage is the main risk factor associated with tree mortality. We recommend the inclusion of protocols that allow the collection of conditions on living trees and follow the fate of these trees to advance the understanding on tree mortality. Approaches based on living trees allow for the inclusion of other potential factors of mortality and their multivariate and interacting nature. Observations based on dead trees are quite limited and rely on assumptions about links between *premortem* conditions and risks that are weakly supported by the data. As tree mortality rates are likely to change with global change, future research should focus on the links between mortality risk factors, their climatic drivers and the physiological mechanisms leading to tree death.

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## Author contributions

DZ, GA, HCM-L, SM and SJD conceptualised the study, performed formal analysis, and contributed to methodology, validation and visualisation. DZ, GA, HCM-L, SA, SB, DC, C-HC-Y, AD, DM, MN, RP, I-FS, YTL and SJD performed data curation and investigation. SJD, SA, DC, C-HC-Y, AD and I-FS contributed to funding acquisition and provided resources. DZ and GA contributed to software. SJD performed supervision. DZ wrote the original draft. All authors wrote, reviewed and edited the manuscript.

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## Data availability

Main data for sites in the ForestGEO plot network are available through the online portal at: <http://www.forestgeo.si.edu>. Data for the annual mortality surveys are available upon request to SJD, DZ, GA and the corresponding Principal Investigators of the ForestGEO site of interest.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Number of individuals and observations in GLMM random-effect groups.

**Fig. S2** Site-level GLMM coefficients for each condition.

**Fig. S3** Distribution of weights used to upscale results to the forest level.

**Fig. S4** Sample-based conditions.

**Fig. S5** Sample-based prevalence, lethality and impact of risk factors.

**Fig. S6** Sample-based prevalence, lethality and impact of *risky* conditions.

**Fig. S7** Site-specific forest-wide prevalence, lethality and impact of risk factors.

**Fig. S8** Forest-wide prevalence, lethality and impact of risk factors on trees  $\geq 100$  mm dbh.

**Fig. S9** Forest-wide prevalence, lethality and impact using a 1.5-fold threshold to define risks.

**Fig. S10** Forest-wide prevalence, lethality and impact using a three-fold threshold to define risks.

**Fig. S11** Sensitivity analysis using different thresholds in the risk definitions.

**Fig. S12** Sensitivity analysis using different minimum taxonomic group sizes.

**Fig. S13** Co-occurrence of risk factors in the rest of risks (complementary to Fig. 4).

**Fig. S14** Co-occurrence of risk factors in trees that subsequently died.

**Methods S1** Crown damage estimates.

**Methods S2** Instantaneous mortality rates.

**Notes S1** GLMMs summary statistics and analysis of residuals.

**Notes S2** ForestGEO site-specific acknowledgements.

**Table S1** ForestGEO site-level characteristics and estimates.

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