

1 **Individual tree damage dominates mortality risk factors across six tropical forests**

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This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/NPH.17832](https://doi.org/10.1111/NPH.17832)

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33 Received: 26 July 2021

34 Accepted: 21 October 2021

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52 **Summary**

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- 54 • The relative importance of tree mortality risk factors remains unknown, especially in
55 diverse tropical forests where species may vary widely in their responses to particular
56 conditions.
- 57 • We present a new framework for quantifying the importance of mortality risk factors and
58 apply it to compare 19 risks on 31,203 trees (1,977 species) in 14 one-year periods in six
59 tropical forests. We defined a condition as a risk factor for a species if it was associated

60 with at least a doubling of mortality rate in univariate analyses. For each risk, we
61 estimated prevalence (frequency), lethality (difference in mortality between trees with
62 and without the risk), and impact (“excess mortality” associated with the risk, relative to
63 stand-level mortality).

- 64 • The most impactful risk factors were light limitation and crown/trunk loss; the most
65 prevalent were light limitation and small size; the most lethal were leaf damage and
66 wounds. Modes of death (standing, broken, and uprooted) had limited links with previous
67 conditions and mortality risk factors.
- 68 • We provide the first ranking of importance of tree-level mortality risk factors in tropical
69 forests. Future research should focus on the links between these risks, their climatic
70 drivers, and the physiological processes to enable mechanistic predictions of future tree
71 mortality.

72

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

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76

77 **Introduction**

78

79 Tree mortality is a key component of forest functioning and dynamics, affecting forest structure,
80 community composition and biogeochemical cycles (Franklin *et al.*, 1987). Recent studies have
81 reported rising tree mortality rates in forests worldwide (Allen *et al.*, 2010; McDowell *et al.*,
82 2020), including the tropics (Hubau *et al.*, 2020). A range of external drivers may lead to
83 increases in tree mortality; e.g., increased disturbance rates, increased drought frequency, or
84 increased herbivore pressure. The underlying mechanisms of individual tree death remain poorly
85 understood, especially in tropical forests. An improved understanding of how mechanisms act
86 and interact to generate mortality patterns will help us to upscale from individual-level processes
87 to global systems and better predict the future behavior of Earth’s ecosystems.

88

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

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

105

106 Despite the diversity of conditions that trees experience in the forest, many studies of tropical
107 forest mortality classify the causes of death into structural vs. physiological factors (Chao *et al.*,
108 2009; Esquivel-Muelbert *et al.*, 2020). Distinguishing between physiological and structural
109 causes of tree death is typically inferred from the physical state of a dead tree, without
110 considering observations prior to death. Trees found dead and broken or uprooted are assumed to
111 have died of structural causes, whereas trees found dead and standing are considered to have died
112 of physiological causes (e.g., Gale & Barfod 1999; Slik 2004; De Toledo *et al.* 2011). By
113 focusing on observations of dead trees, this approach cannot distinguish whether some events
114 occurred before or after the death of the tree (e.g., trunk breakage, leaning, fungal infestation,
115 trunk rot, etc.) and fails to consider some relevant conditions that are not measurable on dead
116 trees (e.g., defoliation, herbivory, light limitation), or disappear rapidly as wood decomposes
117 (e.g., lianas, stranglers, wounds, tumors) (Das *et al.*, 2016; Yanoviak *et al.*, 2019). These
118 problems are exacerbated when the interval between censuses is long, as is common in tropical
119 forest plot monitoring projects (e.g., Davies *et al.* 2021; ForestPlots.net *et al.* 2021). Despite its
120 limitations, the use of *post-mortem* evaluations to infer structural vs. physiological causes of

121 death remains central to large-scale and long-term studies of tropical tree mortality (Chao *et al.*,
122 2009; Esquivel-Muelbert *et al.*, 2020).

123
124 An alternative to the *post-mortem* evaluation is to observe the conditions of living trees, follow
125 them over time, and then assess which conditions are associated with an elevated risk of death to
126 identify mortality risk factors. As this approach requires observations on many living trees and
127 following them to death, the few studies that have assessed multiple mortality risk factors in a
128 time-intensive way have been restricted to small sample sizes and limited geographical areas and
129 environments (Fontes *et al.*, 2018; Aleixo *et al.*, 2019; Preisler *et al.*, 2020). And yet, to elucidate
130 the relative importance of different factors it is critical to simultaneously record data on a broad
131 suite of observations of living trees and monitor subsequent survival. By doing so, it would be
132 possible to assess which mortality risks are most common in tropical forests (prevalence), which
133 most elevate individual mortality (lethality), and which contribute most to overall mortality rates
134 (impact) within and among forests (Box 1). Furthermore, by monitoring the frequency of
135 mortality risks in living trees, it should be possible to detect increases in the frequency of
136 mortality risks before any change in mortality.

137
138 Here, we use annual assessments of survival status and numerous tree-level conditions to identify
139 mortality risk factors and evaluate their relative importance in tropical forests. We used 99,858
140 (individual \times census) sets of observations, each spanning 15 conditions, collected in annual
141 censuses between 2016 and 2020 on 31,203 individual trees of 1,977 species in six tropical
142 forests. Our overarching goal is to provide a ranking of importance of risk factors based on their
143 impact in these tropical forests. We present and apply a new quantitative framework to assign
144 tree mortality risk factors and thereby compare which are most important in terms of their
145 prevalence (frequency of trees affected), their lethality (differences in mortality between trees
146 with and without the risk), and their total impact (proportion of total mortality that is “excess
147 mortality” associated with the risk). We also evaluate the degree to which conditions and
148 mortality risk factors on living trees vary systematically among traditional *post-mortem*
149 assignments of modes of death (i.e., standing, broken, and uprooted).

150

151

152 **Materials and Methods**

153

154 **Study sites**

155

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

164

165 **Sampling design**

166

167 The study included 33,933 stems of 31,203 trees and 1,977 species (2,156 species \times site
168 combinations) (Table S1). In each site, we examined and followed the fate of a cohort of 4,507-
169 8,464 stems (average 5,655) with diameter at the point of measurement (dbh) \geq 10 mm that were
170 alive in the most recent complete census of the plot. Depending on the site, each tree was
171 revisited between two and five times between 2016 and 2020 for a total of 14 one-year census
172 intervals and 99,858 (individual \times census) observations. Trees were selected based on a nested
173 sampling design stratified by habitat and size to capture the diversity of species, the range of tree
174 sizes, topography and other environmental features within plots. Overall, species included in our
175 sample represented 92% of the total number of individuals in these forests. Arellano *et al.* (2021)
176 provide extensive details on the sampling design and field methods.

177

178 **Tree-level conditions**

179

180 The series of observations made on each stem and individual are described in detail in the
181 protocol for the annual mortality surveys of ForestGEO (Arellano *et al.*, 2021). Briefly, for each
182 tree, we recorded: (1) the survival status of the individual (dead/alive); (2) the physical state of

183 each stem (standing, broken, uprooted); (3) the remaining living length in meters along the main
184 axis of the stem; (4) the remaining crown within the living length (%); (5) the illumination index
185 (five levels, from least to most exposed to light); (6) the leaning of the trunk (in degrees); (7)
186 defoliation within the remaining branches (%); (8) infestation by lianas in >50% of the crown
187 (presence/absence); (9) presence of stranglers on the trunk (presence/absence); (10) wounded
188 trunk (three levels); (11) deformed trunk (three levels); (12) rotting trunk (three levels); (13)
189 presence of fungi (presence/absence); and (14) obvious leaf damage (presence/absence). Trees
190 found “broken” and “uprooted” were grouped into the “uprooted” category. Except for survival
191 status, all variables were collected in the field at the stem level. In seasonal forests, censuses
192 were carried out during the wet season to distinguish between defoliation and deciduousness.
193 Added to these 14 variables, we also considered the dbh measured in the previous full census of
194 the plot and the topographic elevation of each tree.

195

196 The only two conditions that required post-fieldwork processing were the trunk loss and crown
197 loss of each stem. We calculated trunk loss and crown loss relative to the ideal trunk and crown,
198 respectively. The ‘ideal’ height of each trunk was estimated from a height-diameter model (eqn.
199 6a in Chave *et al.* 2014), re-scaled at each site to the known local maximum height. Then, the
200 field estimates of remaining living lengths were compared with these ideal heights to estimate
201 the relative trunk loss. To estimate the crown loss we used a model of the cumulative relative
202 volume of tree trunk vs. crown at a relative height r (Ver Planck & Macfarlane, 2014). We used
203 this model to estimate the proportion of crown volume above and below a given height and
204 multiplied it by the relative biomass of the crown ($\frac{1}{3}$ of the total tree biomass; Chambers *et al.*,
205 2001; Duque *et al.*, 2017). Tree biomass was calculated based on the species wood density, the
206 stem dbh, and a site-specific environmental stress variable (Chave *et al.*, 2014; Réjou-Méchain *et*
207 *al.*, 2017). Total crown biomass loss was calculated as [estimated crown biomass above the
208 remaining living length] + [[estimated crown biomass below the living length] \times [1 - estimated
209 proportion of remaining crown within the living length]]. Specific details on the calculation are
210 provided in Methods S1.

211

212 **Assignment of mortality risk factors**

213

214 We made no *a priori* assumptions regarding whether specific conditions represent mortality risk
215 factors. Instead, we defined a condition as a mortality risk for a given species in a given site if
216 the condition more than doubled the predicted probability of death in a fitted univariate model,
217 that is, in a model in which the only fixed effect was the condition. We recognize that conditions
218 are often confounded and that mortality depends on multiple conditions, but our dataset is not yet
219 large enough to enable fitting multivariate models. Thus, we constructed separate Generalized
220 Linear Mixed-Effects Models (GLMMs) for each site and condition to model the probability of
221 death at the end of a given census interval as a function of the tree-level condition at the
222 beginning of the interval. We used a logit link function and random intercepts and slopes
223 depending on the species. GLMMs were fitted by maximum likelihood estimation (Laplace
224 approximation) using the *lme4* package in R (Bates *et al.*, 2015). In *lme4* R notation, the formula
225 was $M \sim 1 + c + (1 + c | s)$, where M is the probability of mortality, and c is the condition of each
226 individual tree of species s at the beginning of a census interval. Each condition c was analyzed
227 separately (Table 1).

228

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

240

241 The predicted probabilities from univariate GLMMs were used as a tool to assign mortality risks
242 to individuals at the beginning of each interval. We first used the predictions from each site-level
243 model to extract the species random slopes and determine which species were positively or
244 negatively affected by each condition (Box 1). We disregarded negative slopes that lacked a

245 plausible biological interpretation (e.g., higher survival under higher levels of crown loss).
246 Second, for each condition c in each site, we defined ‘baseline’ mortality of each species ($mq_{c,s}$)
247 as the lowest modeled mortality probability among individuals of species s . Third, for each
248 census interval t and type of condition c , we predicted the probability of death of each individual
249 i of species s in each site ($mp_{c,s,i,t}$). An individual tree was defined as ‘at risk’ if ($mp_{c,s,i,t}/mq_{c,s}$)
250 > 2 , i.e., if its probability of mortality was more than two-fold higher than the corresponding
251 baseline mortality for its species in its site.

252

253 It is important emphasize that our analyses quantify *univariate associations* between individual
254 conditions and mortality probability (controlling for species identity), and that these associations
255 do not necessarily indicate causal relationships. Our univariate analyses inherently fail to control
256 for other co-occurring conditions, which may be confounded. We initially attempted to perform
257 AIC-based model selection for mortality models including all 15 conditions, their interactions,
258 and species random effects, but these models suffered from model overfitting and convergence
259 issues. We did not explore multivariate models without species random effects because both the
260 literature and our preliminary analyses indicated that species vary strongly in their responses to
261 individual conditions. We considered a variable reduction approach, in which the conditions
262 would be grouped into a few categories (e.g., physiological, environmental and mechanical).
263 However, grouping factors *a priori* was largely arbitrary and conceptually flawed because most
264 of the conditions studied belonged to multiple groups. For example, the presence of lianas could
265 be both a physiological factor (competition for light) or a disturbance/mechanical factor (heavy
266 weight, lateral tensions). Alternatively, grouping conditions *a posteriori* based on patterns of co-
267 occurrence resulted in groups without an intuitive or mechanistic meaning making inferences
268 about risk factors even more complicated. After multiple preliminary analysis and much
269 discussion, we abandoned these alternative approaches and focused on the definition of risk
270 factors from univariate models. The results from univariate models are straightforward to
271 interpret and can inform future experiments and multivariate modeling efforts.

272

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

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

276 Generalized Linear Mixed-Effects Models (GLMM) were constructed to determine whether each
277 condition was a species-specific mortality risk and assign risks to individual trees. Since all

278 variables, except elevation, were obtained at the stem level, conditions were estimated at the
279 individual tree-level as follows: maximum dbh across stems in the individual for the ‘Size’
280 condition; most representative physical state or mode across stems in the individual defined by
281 basal area for the ‘Physical state’ condition; weighted value by the basal area of each stem in the
282 individual for the ‘Illumination index’, ‘Trunk loss’, ‘Crown loss’, ‘Defoliation’, ‘Leaning’,
283 ‘Lianas’, ‘Stranglers’, ‘Wounded trunk’, ‘Deformities on trunk’, and ‘Rotting trunk’ conditions;
284 and the presence of the condition in any stem within the individual for the ‘Fungal infection’ and
285 ‘Leaf damage’ conditions. The physical state of the tree or ‘mode’ condition was analyzed as a
286 categorical variable; the presence of ‘Fungal infection’ and ‘Leaf damage’ were analyzed as
287 binary variables; and the rest of the conditions were analyzed as continuous variables. Symbols
288 (+) and (-) in the third column indicate whether risk factors were defined from species with
289 positive or negative slopes, respectively. Formula in the header of the second column refers to
290 *lme4* R notation to fit the univariate GLMMs, where M is the probability of mortality, and c is
291 the condition of each individual tree of species s at the beginning of a census interval.

292

293 **Prevalence, lethality, and impact of mortality risk factors**

294

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

302

303 Due to the size- and habitat-stratified nature of our sample (Arellano et al. 2021), our estimates
304 cannot be directly extrapolated from the sample to the whole forest. For example, small trees are
305 under-represented in the sample compared to their relative abundance in the forest. The same
306 applies to species representation, with some common species possibly under-represented in our
307 sample due to stratification by habitat. To infer patterns at the full 24-50 ha plot scale from our
308 stratified sample, we assigned weights to each individual in the sample, so that under-represented

309 types of individuals received greater weight than over-represented types of individuals. To do
 310 this, we classified all individuals in the forest and in the sample in discrete [size class ×
 311 taxonomic group] bins. Size class bins were based on the 35 dbh classes used in the sampling
 312 design (Arellano et al. 2021), with limits exactly evenly distributed on a log(dbh) scale: e^x , $x \in$
 313 $\{\ln(10) + 0z, \ln(10) + 1z, \ln(10) + 2z, \dots, \ln(10) + 34z, \infty\}$ and $z = (7 - \ln(10))/34$, in
 314 mm. If a [species × size] bin present in the forest was absent from the sample, we assigned
 315 individuals in the forest to bins based on [genus × size] or [family × size] and/or the most similar
 316 size class. Finally, for each census interval, we assigned to each individual i in the sample a
 317 weight based on its bin equal to $w_i = A/B$, where A is the number of individuals in the forest in
 318 that bin, and B the number of individuals in the sample in that bin. The overall distribution of
 319 weights in each site is provided in Fig. S3. These weights are interpreted as the number of trees
 320 in the full forest plot that each individual in the sample i represents and were used in all of the
 321 analyses to obtain forest-wide estimates. To provide context for our estimates of mortality rates
 322 with and without risk factors, we calculated mean mortality rates for each forest and census
 323 interval using sample bins as ‘subpopulations’ (Eq. 8 in Sheil & May, 1996) (Methods S2).

324

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

337

338

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

$$\begin{aligned}
339 \quad P_s &= \frac{\sum_{i \in [S \cap R]} w_i}{\sum_{i \in S} w_i} \\
340 \quad mr_s &= 1 - \left(1 - \frac{\sum_{i \in [S \cap R \cap D]} w_i}{\sum_{i \in [S \cap R]} w_i} \right)^{\wedge (1/T)} \\
341 \quad mq_s &= 1 - \left(1 - \frac{\sum_{i \in [S \cap Q \cap D]} w_i}{\sum_{i \in [S \cap Q]} w_i} \right)^{\wedge (1/T)} \\
342 \quad L_s &= mr_s - mq_s
\end{aligned}$$

343
344 We then calculated stand-level prevalence (P_{stand}), stand-level lethality (L_{stand}), and stand-level
345 impact (I_{stand}), as:

$$\begin{aligned}
346 \quad P_{stand} &= \sum F_s P_s \\
L_{stand} &= \frac{\sum F_s P_s L_s}{\sum F_s P_s} \\
347 \quad I_{stand} &= \frac{P_{stand} L_{stand}}{\sum (F_s mq_s) + P_{stand} L_{stand}}
\end{aligned}$$

348
349 A worked example of these calculations for the damage condition of trunk broken is shown in
350 Box 1.

351
352 We calculated prevalence, lethality, and impact for each site \times interval, and reported their means
353 and standard deviations. These standard deviations provide a simple first estimate of variability
354 among sites and over time; they do not represent an accounting of the overall uncertainty related
355 to observational error and process variability. We acknowledge that there are many sources of
356 error and uncertainty in our estimates (i.e., field measurements, allometric models, uncertainty in
357 parameter estimation, and the conversion to forest-wide estimates). A full accounting and
358 propagation of these errors is beyond the scope of the current work.

359
360 We evaluated the robustness of our results to details of our methods, and the generality of results
361 across individual sites. Our main analyses upscale our results to all trees ≥ 10 mm dbh in the
362 forest using weights; we also report results just for our observed sample, and when upscaling

363 only trees ≥ 100 mm dbh. We also reported the main results based on arbitrary definitions of
364 “*risky conditions*” in the sample, i.e., not model-informed risk factor assignments. Examples of
365 arbitrary definitions of “*risky conditions*” include the assignment of: a “Crown loss” risk to trees
366 with $>10\%$ loss in the crown; a “Defoliation” risk to trees with $>10\%$ defoliation; etc. Our main
367 analyses define species groups for the GLMM random effects using at least 10 individuals; we
368 fitted models and reproduced the main results for groups with at least 5 and 30 individuals. Our
369 main analyses define a condition as a risk factor if it elevates mortality rates 2-fold within
370 taxonomic groups; we repeated the analyses using 1.5-fold and 3-fold thresholds instead. Finally,
371 we also report results for individual sites, combining census intervals within sites.

372

373 **Co-occurrence of mortality risk factors**

374

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

381

382 **Association of conditions and risk factors with modes of death**

383

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

393

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

395

396

397 **Results**

398

399 The trees we evaluated spanned all topographic positions, light environments, and sizes ≥ 10 mm
400 dbh within each forest (Figs. 1, S4). Most of the trees were standing and upright. Except for
401 being light-limited, most of them had no evidence of conditions expected to negatively affect
402 survival (Fig. 1). We recorded 2,100 tree deaths among our 99,858 observations (tree \times census
403 interval) in 14 one-year census intervals. Upscaling by size class and taxonomic group, this
404 corresponded to average annual forest-wide mortality rates of 2.2% yr⁻¹ (SE = 0.2% yr⁻¹) for
405 trees ≥ 100 mm dbh and 3.9% yr⁻¹ (SE = 0.4% yr⁻¹) for all trees ≥ 10 mm dbh (Table S1).

406

407 Mortality risk factors varied in their prevalence, lethality, and impact (Fig. 2). Light-limitation
408 was the most assigned risk factor (recorded in an average of 72% of trees in a site \times interval),
409 followed by small-tree risk (27%), and damage-related risks: crown loss, trunk loss, and trunk
410 broken (13-20%; Fig. 2a). These highly prevalent risk factors exhibited relatively low lethality
411 (3-11% yr⁻¹; Fig. 2b) but were the most impactful in terms of their contribution to total mortality:
412 53% for light-limitation and 22-45% for damage-related risk factors (Fig. 2c). The most lethal
413 risk factor was leaf damage, which was associated with an increase in mortality rate of 60% per
414 year (that is, a tree that would have had a mortality rate of 3% without leaf damage would have a
415 mortality rate of 63% with leaf damage), followed by wounds, rotting, and uprooting (lethality of
416 19-23% per year; Fig. 2b). However, these highly lethal risks had relatively low impact (<3.1%
417 of mortality), reflecting their low prevalence (<2.5% of trees). Leaning, defoliation, and lower
418 elevation risks were moderately impactful risk factors, each contributing more than 4.5% of total
419 mortality; these were each present in over 4.6% of trees (prevalence) and exhibited lethality of
420 5-14%. Across risk factors, there was a significant correlation between impact and prevalence
421 (Pearson's correlation (r) = 0.86, $P < 0.001$) but no relationship between impact and lethality ($r = -$
422 0.29; $P > 0.05$) or between lethality and prevalence ($r = -0.30$; $P > 0.05$).

423

424 The ranking of importance of risk factors was generally maintained when weights were not used
425 to upscale to the forest-level (i.e., estimates from the sample, Fig. S5), when “*risky conditions*”
426 were defined in a discretionary way instead of being model-informed risks (Fig. S6), when
427 analyses were performed separately for each site (Fig. S7), when only large trees (≥ 100 mm
428 dbh) were analyzed (Fig. S8), when other thresholds were employed in the risk definition (Figs.
429 S9, S10, S11), or when mortality models employed to define risks used different minimum
430 taxonomic group sizes (Fig. S12).

431
432 Overall, we found that 82% of all living trees had at least one risk factor, with 44% of these trees
433 having only one risk, and the others having between two and nine risk factors (Fig. 3a). The
434 estimated forest-wide mortality rates for trees without risk factors was $2.2\% \text{ yr}^{-1}$ (SE = $0.6\% \text{ yr}^{-1}$)
435 1), compared with $5.1\% \text{ yr}^{-1}$ (SE = $0.7\% \text{ yr}^{-1}$) for trees with one or more risks. Mortality rates
436 increased with the number of assigned risks, from $2\% \text{ yr}^{-1}$ for trees with one risk to $33\% \text{ yr}^{-1}$ for
437 trees with nine risks (Fig. 3b). The 82% of trees with one or more risk factors accounted for 91%
438 of the overall mortality (or $3.6\% \text{ yr}^{-1}$ forest-wide mortality), whereas the 18% of trees with no
439 assigned mortality risks accounted for 9% of the overall mortality (or $0.3\% \text{ yr}^{-1}$ forest-wide
440 mortality; Fig. 3c). Eighty-seven percent of the dead trees in the forests were trees that had had
441 between one and five risks at the beginning of the interval (Fig. 3c). Co-occurrence of pairs of
442 risk factors largely followed expectations based on the prevalence of individual risk factors, but
443 there were some risks that were disproportionately more likely to co-occur (e.g., combinations of
444 the damage-related risks) (Fig. 4).

445
446 There was very limited systematic variation in conditions across the modes of death and in risk
447 factors across the modes of death (Figs. 5,6) mainly due to the high level of co-occurrence of risk
448 factors in any given mode (Figs. 4,6). Of the 2,100 trees found dead across the 14 intervals, 36%,
449 28%, 11%, and 25% were found standing, broken, uprooted, and with an unidentified mode,
450 respectively. For the 15% of dead trees (308) that were not assigned any risk factors while still
451 alive, 37%, 29%, 11%, and 22% died standing, broken, uprooted, and with an unidentified mode
452 of death, respectively (Fig. 6b). Dead uprooted trees had the most different conditions and risk
453 factors while alive: they were significantly larger, tended to be located at lower elevations, had
454 lower values of trunk and crown damage, and were more leaning than dead standing and dead

455 broken trees. Dead broken and standing trees were not different in their size or elevational
456 location; but dead broken trees had significantly higher trunk and crown damage than standing
457 and uprooted trees (Fig. 5). Consequently, the proportion of dead trees that were assigned the
458 trunk/crown loss risk factors was higher for dead broken than for dead standing or uprooted trees
459 (Fig. 6). Differences in illumination values, the presence of fungal infections, and wounds as
460 well as their associated risk factors across the modes of death were mainly driven by trees with
461 unidentified modes (Fig 5), which were mostly composed by small, light-limited trees and had
462 the lowest incidence of fungal infections and wounds conditions (Fig. 6).

463

464 **Discussion**

465

466 **Relative importance of tree-level mortality risk factors**

467

468 The most important mortality risk factors, by impact, were those related to crown/trunk loss,
469 light limitation, and small size. Leaning, defoliation, and lower elevation ranked next in impact,
470 whereas other risks expected to be important such as those associated with lianas, stranglers,
471 trunk deformities, and trunk rot were not prevalent or impactful in this study. This ranking
472 should inform research priorities and model experiments to improve predictions of the fate of
473 forests in global dynamic vegetation models (McDowell, 2018; Longo *et al.*, 2019; Pugh *et al.*,
474 2020). For example, the measurement of the physiological consequences i.e., carbon starvation
475 and hydraulic failure, across trees with different levels of damage can help to predict the biomass
476 consequences of specific disturbance types in tropical forests.

477

478 Conditions associated with resource availability (light limitation, small tree size, and, to a lesser
479 extent, topographic position) played an important role among the risk factors studied. Light is an
480 important limiting factor related to tree death (Hubbell *et al.*, 1999; Wright *et al.*, 2015). Light-
481 limited trees, which are mostly small (Fig. 4), are expected to die more by competition than large
482 and fully exposed trees (Coomes *et al.*, 2003; Muller-Landau *et al.*, 2006). They also have lower
483 photosynthetic rates that may lead to death following the depletion of non-structural
484 carbohydrates (Kobe, 1997; Poorter & Kitajima, 2007), and are more likely to be impacted by
485 falling branches and neighboring trees (Fig. 4). Because our analyses were weighted to be

486 representative of all trees with $\text{dbh} \geq 1$ cm, most trees were light-limited, and this risk factor had
487 the highest prevalence as well as the highest impact (Fig. 2). Even when restricting analyses to
488 trees with $\text{dbh} \geq 10$ cm, light limitation still had the highest prevalence and the second-highest
489 impact (Fig S8). However, it is important to clarify that the frequency of a condition in the forest
490 and the impact of the associated risk factor are not necessarily correlated, as this relationship is
491 mediated by both the species-level sensitivities to the conditions and the lethality of the risk
492 when it is present (Box 1).

493

494 Being at lower elevations than the average for a given species was associated with a higher risk
495 of mortality than being at higher elevations. Variation in below-ground resources, in contrast
496 with light-limitation, is largely determined by topography, and leads to variation in individual-
497 level performance among topographically defined habitats (Bunyavejchewin *et al.*, 2019; Zuleta
498 *et al.*, 2020). Although lower-elevation locations or valleys are generally wetter than slopes or
499 ridges, trees in valleys face flooding more frequently (Margrove *et al.*, 2015; Moser *et al.*, 2019)
500 and are sensitive to extreme water shortage because tend to prioritize efficient water transport
501 over hydraulic safety (Zuleta *et al.*, 2017; Cosme *et al.*, 2017). That said, topographic-related
502 risks were particularly variable across sites (see below; Fig. S7).

503

504 Trees with crown or trunk damage in the previous census had an impact on forest mortality of
505 22-45%. The importance of these risks results from both their high prevalence (13-20%) and
506 moderate lethality (8-11%). Damaged trees are more prone to die because of the loss of
507 photosynthetic capacity, large energetic costs of repair (Anderegg *et al.*, 2012; Trugman *et al.*,
508 2018; Arellano *et al.*, 2019), and increased exposure to pathogens and pests (Dyer *et al.*, 2012).
509 Trunk and crown damage may result from mechanical stress (e.g., wind, storms, branch fall,
510 treefall, lightning, etc.) or the decay of standing trees due to physiological stress (e.g., resource
511 limitation, drought, herbivory, etc.), or some combination of both. Observational studies such as
512 this one cannot disentangle losses due to physiological vs. mechanical causes. The relatively
513 moderate lethality of damage-related risks compared to other risks such as leaf damage, fungal
514 infections, or defoliation indicates that an important proportion of damaged trees can survive
515 from year to year. Indeed, trees are capable of recovering following structural or physiological
516 damage (Ruslandi *et al.*, 2012; Anderegg *et al.*, 2015; Shenkin *et al.*, 2015; Magnabosco Marra

517 *et al.*, 2018; Kannenberg *et al.*, 2020). As modular organisms, trees can delay death or recover by
518 compartmentalizing damage (Shigo, 1984; Finch, 1990; Bernard *et al.*, 2020). This trait along
519 with the ability to resprout constitute key traits that allow trees to withstand damage (Putz &
520 Brokaw, 1989; Paciorek *et al.*, 2000; Su *et al.*, 2020).

521
522 After risks related to resource limitation and wood damage, leaning and defoliation were the next
523 most important risk factors experienced by trees. A leaning trunk is more vulnerable to breakage
524 and/or uprooting (Fig. 4), and can imply suboptimal allocation given that more wood is required
525 for the same absolute height growth (Fournier *et al.*, 2006; Bragg & Shelton, 2010; Shenkin *et*
526 *al.*, 2015). Given the relatively high prevalence of this risk factor, studies that remove leaning
527 trees to estimate demographic rates are likely biased towards healthier-than-average trees (e.g.,
528 Lieberman *et al.* 1985; Visser *et al.* 2016). Defoliation, on the other hand, was rarely recorded in
529 the field (Fig. 1g), but the high lethality associated with this condition resulted in moderate
530 impact. The role of defoliation on mortality has been widely shown in temperate forests
531 (Dobbertin, 2005); here we provide the first evidence for its importance in tropical forests.
532 Although death in a defoliated tree may have resulted from reduced photosynthesis and induced
533 carbon starvation, defoliation can also be a symptom or consequence of other mechanisms killing
534 a tree (Fig. 4).

535
536 Although the forests included in this study differ in composition and environmental conditions,
537 the relative importance of the main risk factors were similar (Fig. S7; also evidenced from error
538 bars in Fig. 2). Even the estimated coefficients in the mortality models employed to assign these
539 risks reflect consistent effects across sites (Fig. S2). Risks related to topographic conditions and
540 size (and their associated models) were the most variable among sites. “Lower elevation” was
541 assigned as a risk factor only in Amacayacu (Colombia), HKK (Thailand), and Pasoh
542 (Malaysia); while the “smaller tree” risk was more important in HKK and KC (Thailand), and in
543 Fushan (Taiwan). These differences may be a consequence of the different local impact of El
544 Niño related droughts in 2015-16, which are expected to leave a topography and tree size
545 signature (Zuleta *et al.*, 2017; Gora & Esquivel-muelbert, 2021). Unfortunately, our time series
546 were not enough to study the relationship between climate and mortality patterns. The continued
547 monitoring of conditions of living trees and their fate under ongoing climatic changes will enable

548 the assessment of climate-related mortality risks and their multivariate interactions with the tree-
549 individual mortality risk factors studied here.

550

551 **The limited inference from modes of death**

552

553 *Post-mortem* designation of modes of death has been the standard method for inferring mortality
554 mechanisms in observational studies, where dead standing and dead broken/uprooted have been
555 attributed to physiological and mechanical causes of death, respectively (Chao et al., 2009; De
556 Toledo et al., 2011; Gale and Barfod, 1999; Slik, 2004). Using this approach, for example, half
557 of the deaths in neotropical forests were recently attributed to mechanical damage caused by
558 winds or storms, and the other half to physiological mechanisms such as competition for
559 resources or drought stress (Esquivel-Muelbert et al., 2020). Our analyses of the relationship
560 between the modes of death and the conditions and risk factors of the same trees before they died
561 suggest very limited evidence for the assumptions implicit in the *post-mortem* approach. For
562 example, we may have expected light-limited trees to die mostly standing, but the proportion of
563 dead trees with low values of illumination index was higher among broken than standing dead
564 trees (Fig. 5c). These results are largely driven by the high levels of co-occurrence among risk
565 factors (Figs. 4,6). Even in cases in which statistically significant differences in the conditions
566 were found across modes of death (e.g., dead uprooted trees had higher values of leaning before
567 dying, and dead broken trees had higher trunk and crown damage before dying), trees found dead
568 with a specific mode share many pre-death conditions and risk factors that often result from a
569 mix of mechanical and physiological stressors (Fig. 6; Franklin et al. 1987; Das et al. 2016).
570 Substantial proportions of dead trees found broken and uprooted have been reported with
571 preexisting fungal infections and/or wood rotting in temperate forests (Larson and Franklin, 2010
572 and references therein). The limited inference from modes of death is reinforced in tropical
573 forests, where the high rates of wood decomposition quickly remove signs of the killing agent
574 (Wieder et al., 2009; Gora et al., 2019) and the interval between forest censuses is typically long
575 and highly variable (e.g., Davies et al. 2021; ForestPlots.net et al. 2021). We therefore urge
576 caution in the inference of tree mortality mechanisms using *post-mortem* surveys.

577

578 **Predicting short-term tropical tree mortality**

579

580 Ninety-one percent of trees that died in these forests had at least one risk factor one year before
581 being found dead. These results suggest that, typically, tree death is not an immediate event due
582 to unpredictable episodic disturbances, but the result of chronic or lagged mechanisms that take
583 some time to develop and kill the tree (Espírito-Santo *et al.*, 2014; Fontes *et al.*, 2018; Arellano
584 *et al.*, 2019; Griffiths *et al.*, 2021). If death is slow and deterministic, rather than sudden and
585 stochastic, then it may be predictable at the individual level. Individual-level mortality models
586 could better represent mortality rates by including the most important processes linked to the
587 tree-level conditions studied here.

588

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

606

607 **Conclusion**

608

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

620
621

622 **Acknowledgments**

623

624 We thank the editor and three anonymous reviewers for providing valuable comments that
625 significantly improved the overall quality of the work. This project and D.Z. were supported as
626 part of the Next Generation Ecosystem Experiments-Tropics, funded by the U.S. Department of
627 Energy, Office of Science, Office of Biological and Environmental Research (<https://ngee-tropics.lbl.gov/>). Data collection was supported by the Forest Global Earth Observatory
628 (ForestGEO) of the Smithsonian Institution. We thank David Bauman for edits and comments on
629 the manuscript. Detailed site-specific acknowledgments are included as Notes S2.

630

631 **Authorship**

632

633
634 The following list describes author participation according to CRediT roles. Conceptualization,
635 Formal Analysis, Methodology, Validation, Visualization: D.Z., G.A., H.C.M-L, S.M., S.J.D.
636 Data curation and Investigation: D.Z., G.A., H.C.M-L, S.A., S.B., D.C., C-H.C-Y., A.D., D.M,
637 M.N., R.P., I-F.S., Y.T.L., S.J.D. Funding acquisition, Resources: S.J.D., S.A., D.C., C-H.C-Y.,
638 A.D., I-F.S. Software: D.Z., G.A. Supervision: S.J.D. Writing – original draft: D.Z. Writing –
639 review & editing: all authors.

640

641 **Data availability**

642

643 Main data for sites in the ForestGEO plot network are available through the online portal at:
644 <http://www.forestgeo.si.edu>. Data for the Annual Mortality Surveys are available upon request to
645 S.J.D, D.Z., G.A, and the corresponding Principal Investigators of the ForestGEO site of interest.

646

647 **Figure legends**

648

649 **Box 1. Definition of prevalence, lethality, and impact of tree mortality risk factors. A**

650 worked example for the condition of physical damage (trunk broken).

651

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

670

671 **Fig. 2.** Estimated forest-wide prevalence, mortality, and impact of 19 risk factors assessed during
672 14 one-year census intervals in six tropical forests. Prevalence (a) is the estimated proportion of
673 individuals in the forest with the risk factor at the beginning of the interval. The lethality (b) is
674 the difference between the mortality rate of individuals *with* a given risk factor and the mortality
675 rate of individuals *without* the risk factor. The impact (c) is the proportion of total mortality in
676 the forest that is “excess mortality” associated with the risk factor, i.e., the estimated percent of
677 mortality that would not have occurred if the risk factor is not present in the forest. Note that
678 having a risk factor means that the tree both had the condition and was estimated to have a
679 mortality rate elevated more than two-fold the baseline because of it. Risk factors are ranked by
680 impact. Error bars are standard errors estimated from the 14 site by census interval combinations
681 among the six sites. All values are based on extrapolating from the observed sample to all trees \geq
682 10 mm dbh in the forest as a whole, with extrapolation based on weighting factors accounting for
683 differences in abundances across classes defined by combinations of dbh and taxonomic group.
684 Estimates based on the sample (i.e., not upscaled to the forest-level) are provided in Fig. S5.
685 Estimates based on arbitrary definitions of “*risky conditions*” in the sample, not model-informed
686 risk factor assignments, are provided in Fig. S6. Estimates for each site, for large trees (≥ 100
687 mm dbh), and using other thresholds in the definition of risks are presented in Figs. S7-S10.

688
689 **Fig. 3.** Estimated forest-wide proportion of trees, mortality, and percent of total mortality for
690 trees with zero to nine risk factors across 14 site by census interval combinations in six tropical
691 forest sites. Values in (a) show the proportion of individuals in the forest with a given number of
692 risk factors (including no risks, 0) at the beginning of the interval. Mortality (b) is the proportion
693 of individuals that died during the census interval among those that started the interval with a
694 given number of risk factors. The percent of total mortality (c) is the proportion of dead
695 individuals in the forest that had a given number of risk factors at the beginning of the interval
696 (grey bars). For reference, empty bars in panel (c) show the proportion of trees with the risk.
697 Error bars are standard errors estimated from the 14 census intervals among the six sites.
698 Numbers above bars indicate the exact percentage. All values are based on extrapolating from
699 the observed sample to all trees ≥ 10 mm dbh in the forest as a whole, with extrapolation based
700 on weighting factors accounting for differences in abundances across classes defined by
701 combinations of dbh and taxonomic group.

702

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

710

711 **Fig. 5.** Frequencies of tree-level conditions of living trees that were subsequently (in the next
712 census) found dead standing (S), broken (B), uprooted (U), or with an unidentified (?) mode of
713 death in six tropical forests. The “Unidentified” mode of death refers to trees for which only the
714 tag was found because they fully decomposed or were beneath fallen trees in a gap. Different
715 letters above bars indicate significant differences in the conditions among the modes of death for
716 continuous variables (a,b,e-h; Wilcoxon rank sum after Kruskal-Wallis tests), and differences in
717 the proportion of dead trees in each group for categorical and binary variables (c,d,i-o; chi-square
718 tests). ‘ns’ indicates non-significant differences. Conditions of surviving trees (“A” for Alive) are
719 also shown for reference but not tested for differences. In the legend of (d), “S” refers to
720 standing; “B” to broken, “U” to uprooted, and “?” to unidentified *physical states* in *living trees*.
721 The “Unidentified” physical state in living trees refers to cases in which the field crews were
722 uncertain. Violin plots in (a,b,e-h) show the distribution of measured values within each mode of
723 death: white circles indicate the mean and the shape as a whole indicates the full distribution of
724 values. Violin plots are truncated according to the range of the variable: at zero for (a,e-h), and at
725 100% for (e-g). In categorical and binary variables (c,d,i-o), the width of each bar is scaled to the
726 proportion of the population in the given category (36% dead standing, 28% broken, 11%
727 uprooted, and 25% unidentified, respectively).

728

729 **Fig. 6.** Frequencies of given mortality risk factors assigned based on prior conditions among
730 trees subsequently (in the next census) found dead standing (S), broken (B), uprooted (U), or in
731 an unidentified (?) mode of death in six tropical forests. The “Unidentified” mode of death refers
732 to trees for which only the tag was found because they fully decomposed or were beneath fallen

733 trees in a gap. Chord-diagram in (a) shows the association between modes of death and risk
734 factors. The lower half of the circle corresponds to the 2,100 dead trees without risks or with
735 each of the 19 risk factors, while the upper half section indicates their modes of death after one
736 year. The arc of the circle in the upper half section corresponds to the proportion of trees found
737 dead standing, broken, uprooted, and with an unidentified mode of death. Colors of the links
738 indicate different risk factors and the width of the link (chord) is proportional to the number of
739 trees. Specific proportions across modes of death are shown in panels (b-n) for trees without
740 risks (b) and for risk factors with at least 50 dead trees (c-n). Dark grey and light-grey colors of
741 the bars correspond to trees with and without the given risk, respectively. P-values above the
742 bars indicate significant differences among modes of death (chi-square tests). “ns” indicates non-
743 significant differences. The width of each bar is scaled to the proportion of the population in the
744 given category (36% dead standing, 28% broken, 11% uprooted, and 25% unidentified,
745 respectively). Numbers in parentheses in (b-n) show the total dead trees with the given risk.
746

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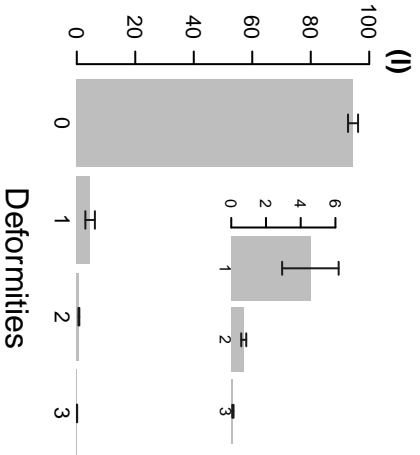
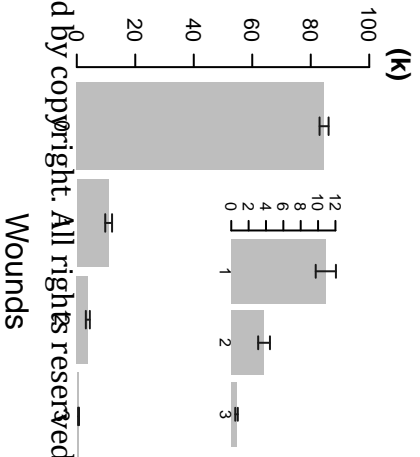
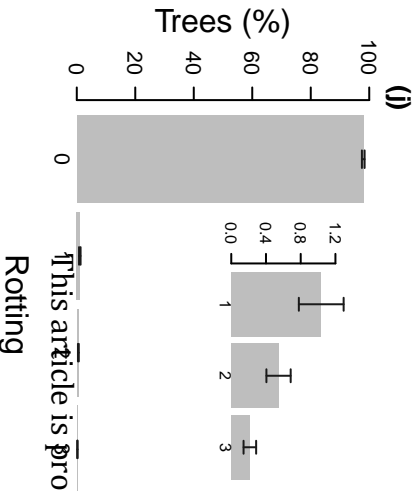
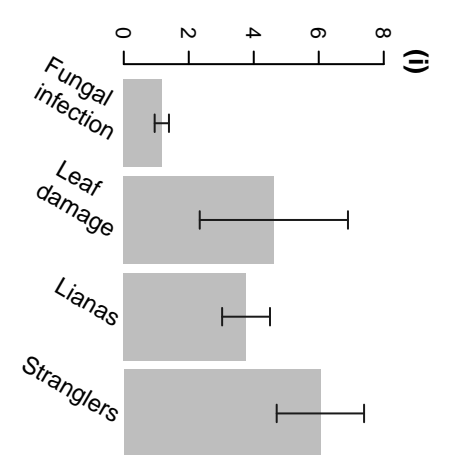
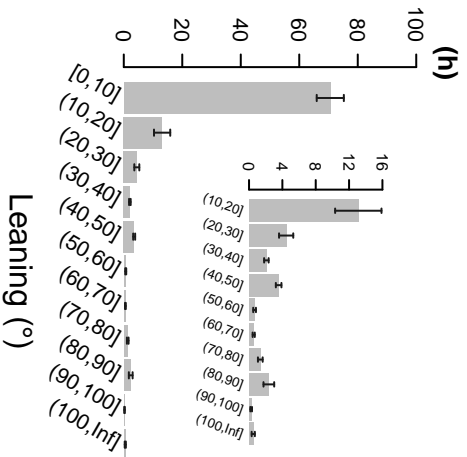
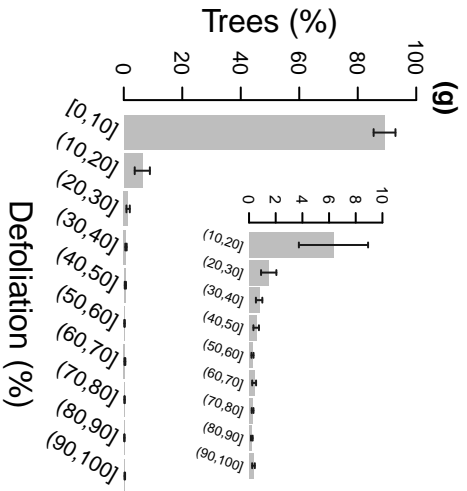
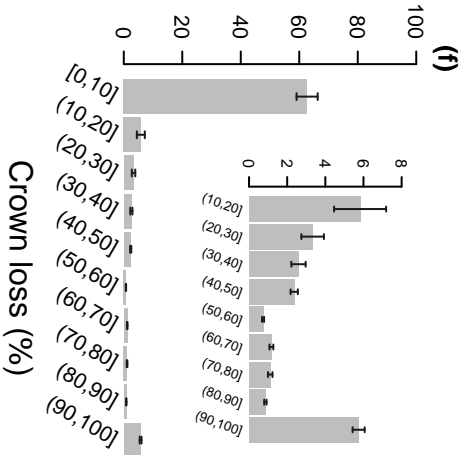
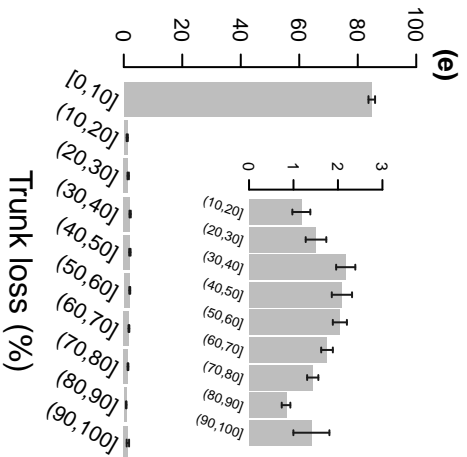
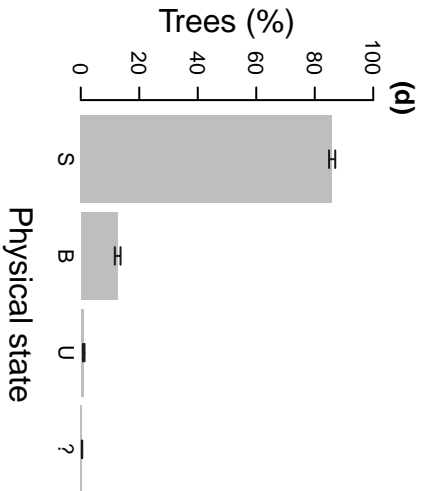
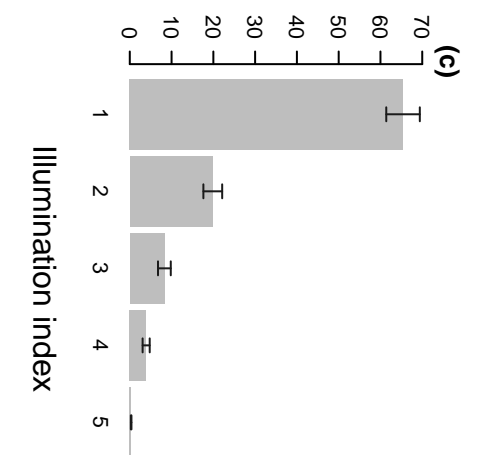
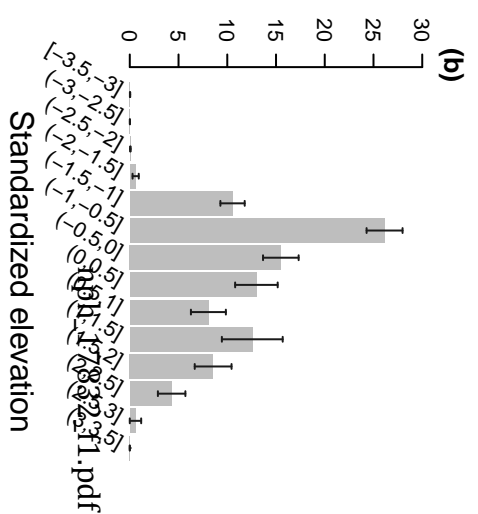
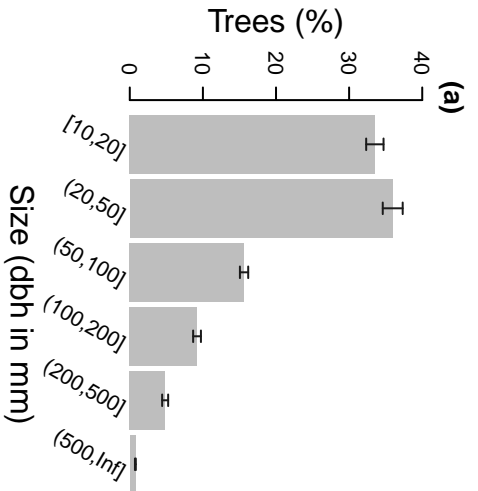
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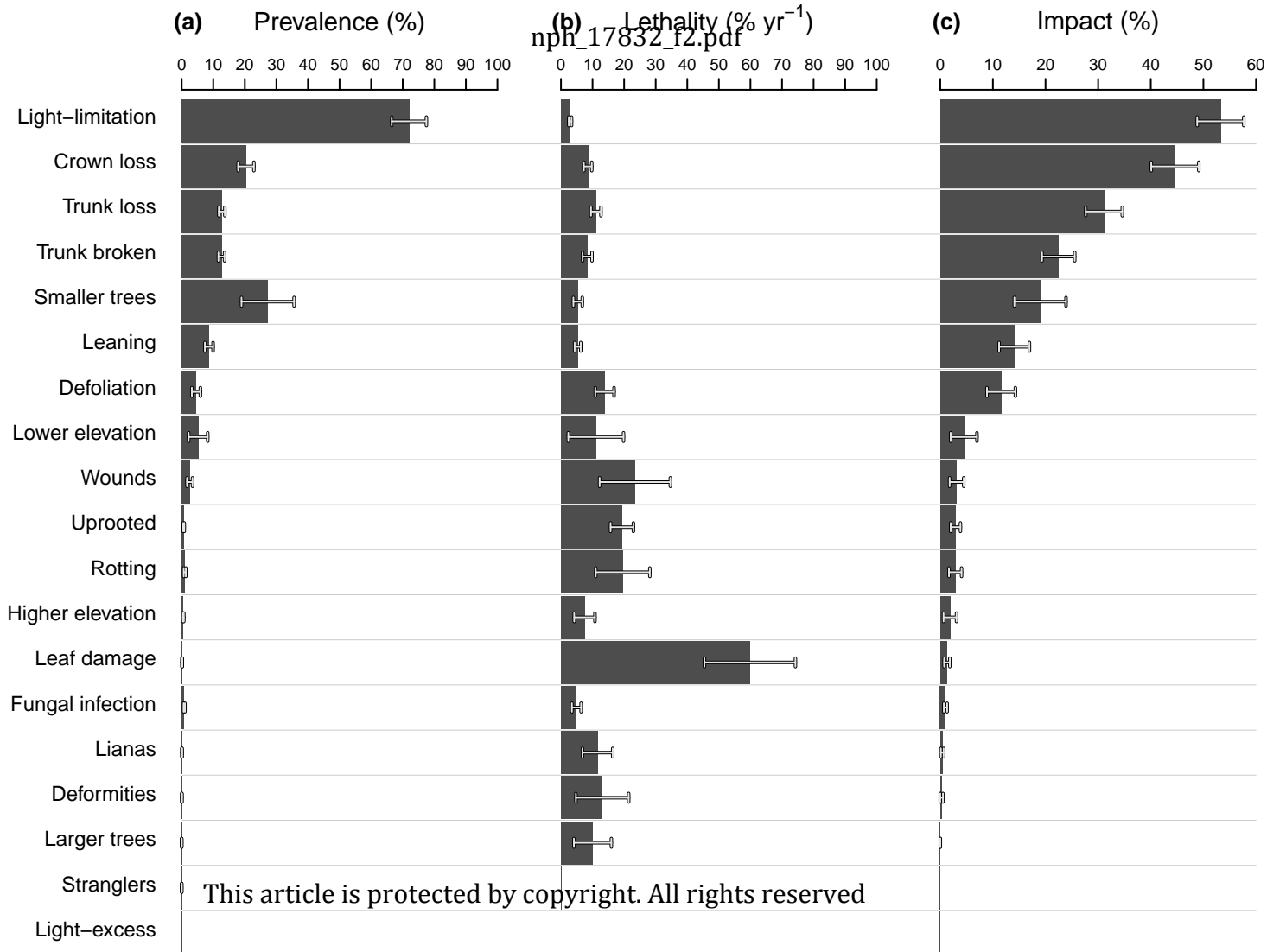
947 **Supporting information – content**

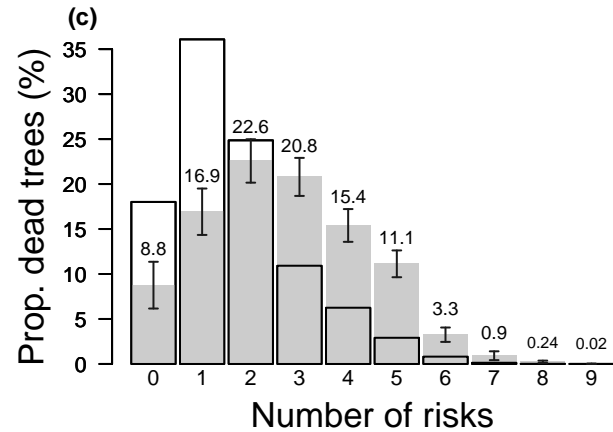
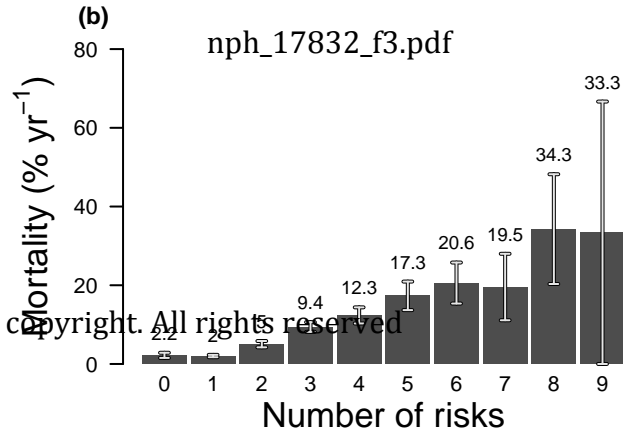
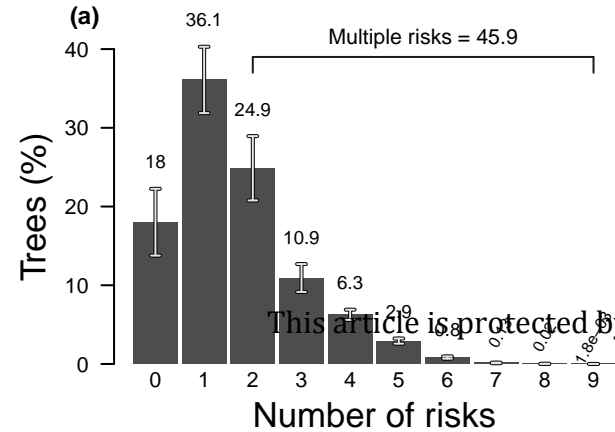
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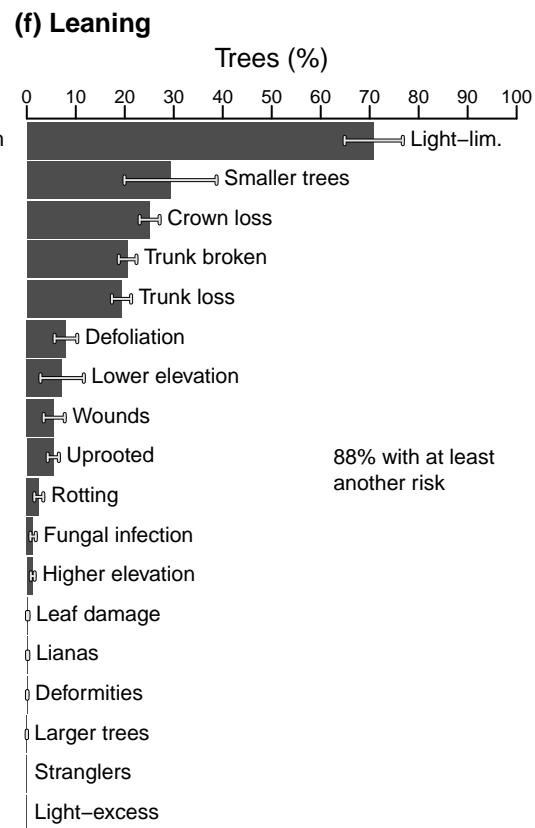
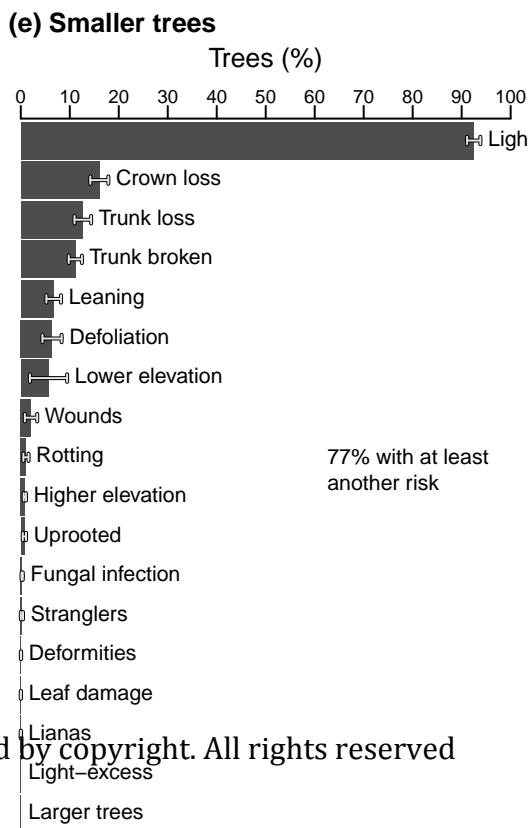
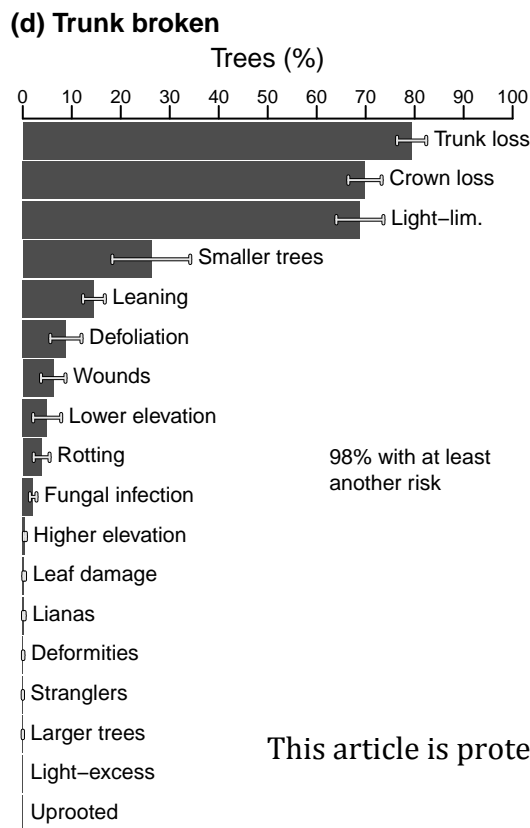
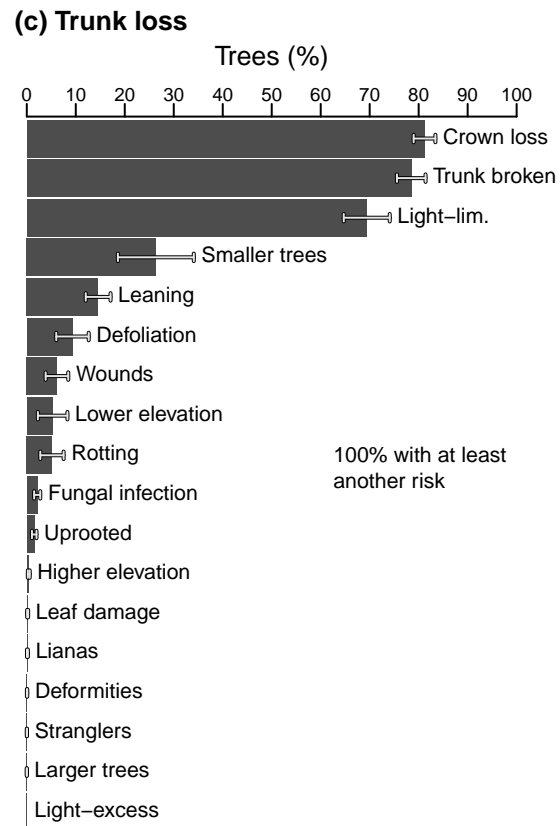
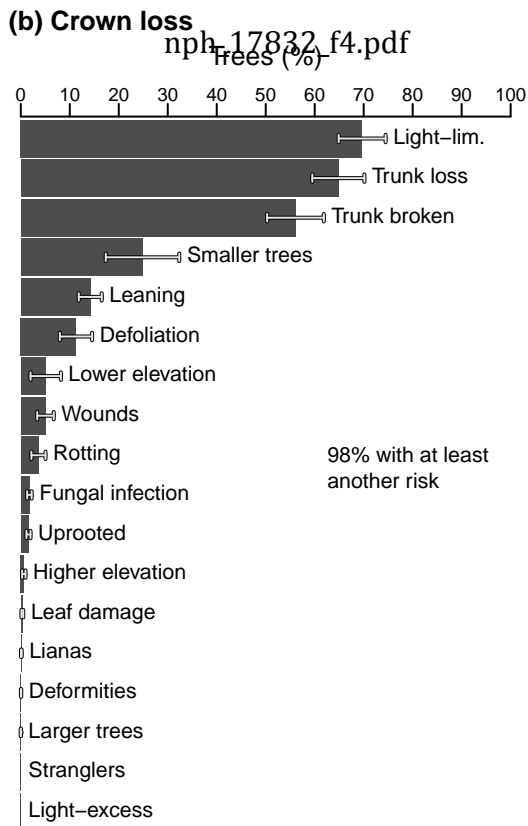
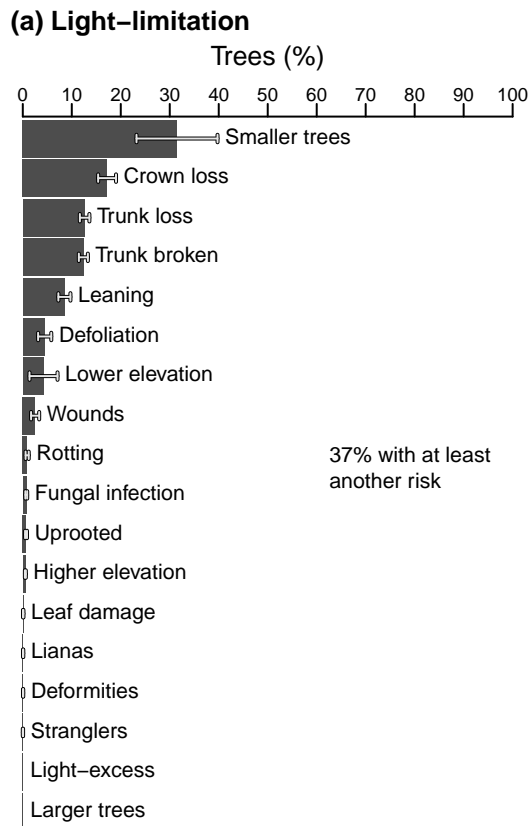
949 **Table S1.** ForestGEO site-level characteristics and estimates.

950 **Fig. S1** No. individuals and observations in GLMM random-effect groups.
951 **Fig. S2** Site-level GLMM coefficients for each condition.
952 **Fig. S3** Distribution of weights used to upscale results to the forest level.
953 **Fig. S4** Sample-based conditions.
954 **Fig. S5** Sample-based prevalence, lethality, and impact of risk factors.
955 **Fig. S6** Sample-based prevalence, lethality, and impact of *risky* conditions.
956 **Fig. S7** Site-specific forest-wide prevalence, lethality, and impact of risk factors.
957 **Fig. S8** Forest-wide prevalence, lethality, and impact of risk factors on trees ≥ 100 mm
958 dbh.
959 **Fig. S9** Forest-wide prevalence, lethality, and impact using a 1.5-fold threshold to define
960 risks.
961 **Fig. S10** Forest-wide prevalence, lethality, and impact using a three-fold threshold to
962 define risks.
963 **Fig. S11** Sensitivity analysis using different thresholds in the risk definitions.
964 **Fig. S12** Sensitivity analysis using different minimum taxonomic group sizes.
965 **Fig. S13** Co-occurrence of risk factors in the rest of risks (complementary to Fig. 4).
966 **Fig. S14** Co-occurrence of risk factors in trees that subsequently died.
967 **Methods S1.** Crown damage estimates.
968 **Methods S2.** Instantaneous mortality rates.
969 **Notes S1.** GLMMs summary statistics and analysis of residuals.
970 **Notes S2.** ForestGEO site-specific acknowledgments.

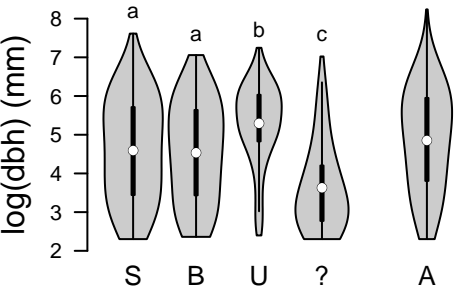




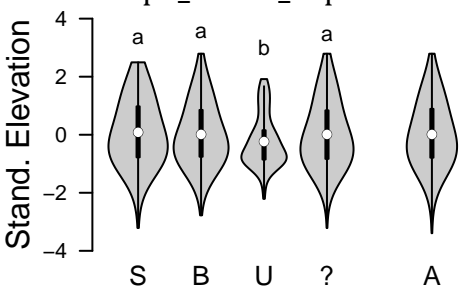




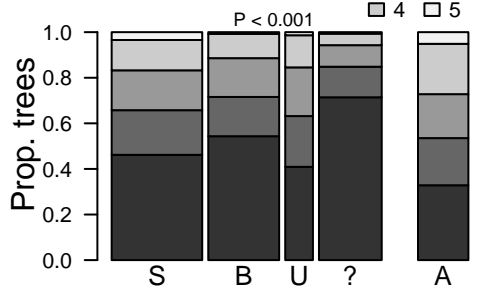
(a) Tree size



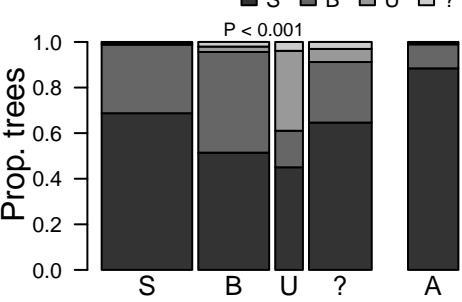
(b) Elevation



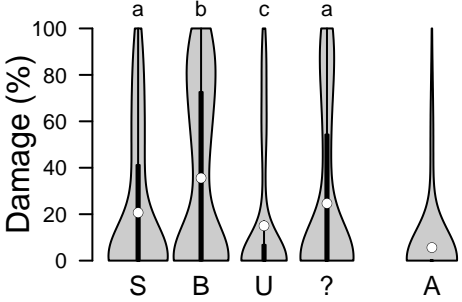
(c) Illumination



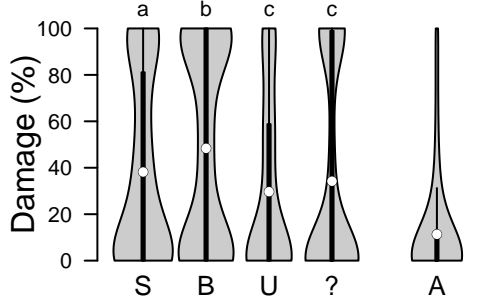
(d) Physical state



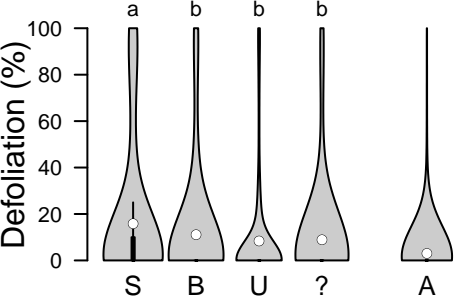
(e) Trunk damage



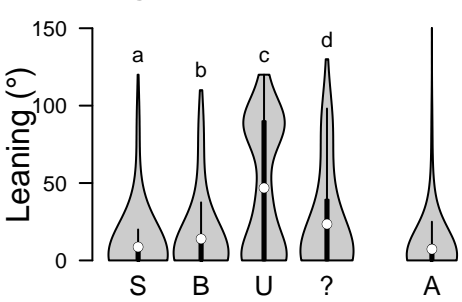
(f) Crown damage



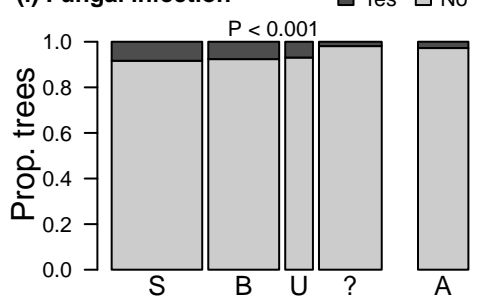
(g) Defoliation



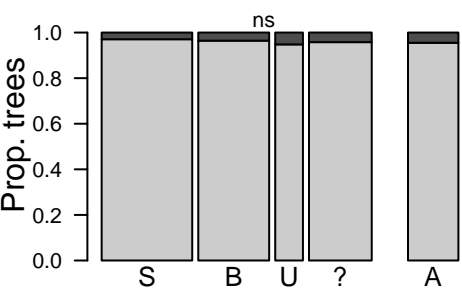
(h) Leaning



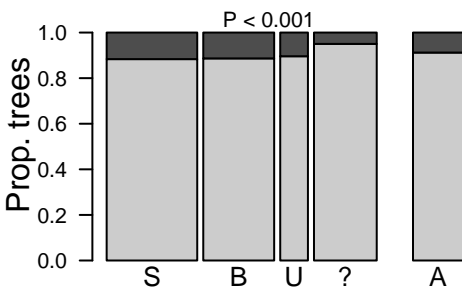
(i) Fungal infection



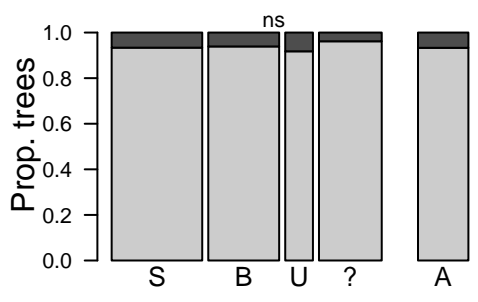
(j) Leaf damage



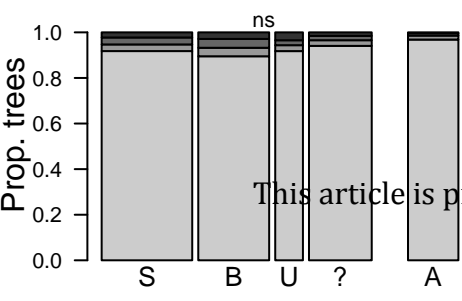
(k) Liana infestation



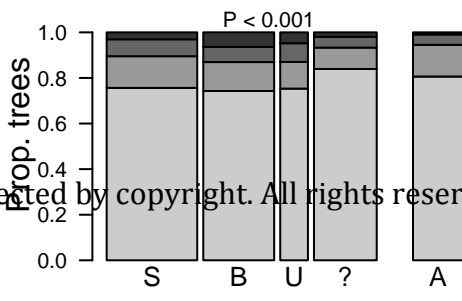
(l) Stranglers



(m) Rotting



(n) Wounds



(o) Deformities

