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Disentangling fire intensity and species' susceptibility to fire in a species-rich seasonal tropical forest

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Abstract

1. Increasing temperatures and human activity are likely to reduce fire return intervals in the seasonal tropics. Anticipating how more frequent fires may alter forest community structure and composition requires understanding how fire intensity and species-specific responses to fires interact to drive fire-induced mortality for large numbers of species. We developed an analytical framework to estimate unobserved fire intensities and species- and size-specific susceptibility to fire using observed mortality data.
2. We used census data from a 50-ha forest dynamics plot in western Thailand to better understand species and community responses to a fire that burned ~60% of the plot in 2005. Trees species, size, and status (live, dead) were censused just before the fire (2004) and again five years later (2009). We jointly estimated a map of relative fire intensity and species-specific size-dependent background and fire-induced mortality. We then calculated the time required for individuals of each species to reach a fire-safe size threshold (the age at which the fire-induced mortality probability was < 50%). To better understand community-level responses to fire, we compared results among different species groups (canopy status, forest-type association).
3. Our model-derived map of fire intensity closely matched the field survey taken in the days after the fire. On average, individuals growing at the 95th percentile growth rate for most species groups required ~5 years to reach their species' fire-safe size threshold, while individuals growing at the median growth rate required ~17 years (assuming growth < 1 cm DBH was similar to growth > 1 cm). However, understorey species associated with the seasonal evergreen forest took 1.8 times longer than average to reach their fire-safe size threshold, with one species requiring up to 190 years.
4. *Synthesis.* Our approach provided insights into spatial patterning of fire intensity in a seasonal tropical forest and species- and size-specific susceptibility to fire-induced mortality. Our results suggest increasing fire frequency will have the greatest impact on slow-growing understorey species of the evergreen forest. In addition, our model accurately predicts the growing dominance of a fast-growing understorey species, *Croton roxburghii*; *Euphorbiaceae*, common to evergreen and deciduous forests that can reach its fire-safe size threshold in 1.3 years.

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Introduction

In the species-rich forests of the seasonal tropics, fires are an important driver of community composition and structure at local scales and the distribution of different forest types at landscape scales. Fires shape community composition by removing individuals of particular species and community structure by removing individuals of particular sizes. The impacts of global change on fire regimes—particularly fire frequency—may have profound and persistent consequences on forest communities and their associated biodiversity by removing individuals and size classes that are more susceptible to fire-induced mortality (Charles-Dominique *et al.*, 2017, Pellegrini *et al.*, 2017). Climate models predict an increase in weather conditions suitable for fire over the next century across many parts of the world (Jolly *et al.*, 2015, Liu *et al.*, 2010, Pechony and Shindell, 2010). Increasing levels of forest fragmentation and associated human activity at the margins of forested landscapes means that the risk of ignition during these extreme fire weather conditions is also higher than in the past. In the seasonal tropics, where both of these trends are well documented, fire return intervals are expected to drop sharply (Scholze *et al.*, 2006).

Forecasting the impacts of changing fire regimes requires understanding which trees are likely to experience fire-induced mortality and how species vary in their resilience to more frequent fires. In general, the probability that a tree is killed by a fire depends on two things: 1) the susceptibility of a tree to a fire of a given intensity and 2) the intensity of the fire. Susceptibility to fire-induced mortality is typically a function of species and tree size. For a given tree size, some species are more likely to be killed than others, whereas for a given species, some trees (usually smaller ones) are more likely to be killed than others. However, susceptibility is difficult to quantify without some independent assessment of fire intensity (*sensu* Keeley, 2009, *i.e.*, the amount of energy in the fire), which is almost never directly observed. In most cases, studies of fire impacts are made in the aftermath of the fire and focus on the outcome (*i.e.*, did this tree die or not?), which necessarily conflates the relative contributions of individual tree *susceptibility* and disturbance *intensity*. This obscures the interactions between fire intensity and tree species mortality that drive forest structure and composition. In addition, to understand which species will or will not be impacted by shorter fire return intervals, it is important to account for the temporal dynamics of susceptibility. While species may vary in the size thresholds at which the probability of fire-induced mortality is low, interspecific differences in growth rates may either exacerbate or eliminate these differences. For example, a thin-barked tree species may need to reach a much larger stem diameter than a thick-barked species to be safe from fire-induced mortality; however, if the thin-barked species is much faster growing, the total amount of time that individuals from each species are exposed to the risk of mortality from fire may be the same. This is similar to the concept of passage time in plant population biology, which estimates the length of time required for an individual to reach canopy size (*e.g.*, Clark and Clark, 1992, Needham *et al.*, 2018). Here our interest is in the time required to reach a fire-safe size relative to the current and future fire return intervals.

We developed an analytical framework to make quantitative estimates of unobserved fire intensity and unknown species susceptibility to fire using observed mortality data. We took advantage of a large-scale, long-term forest dynamics plot in western Thailand that was partially burned in 2005 and that, at that time, had been the focus of intensive study for more than a decade. We used latent variable modelling to simultaneously estimate the intensity of the fire within the plot and the sensitivity to fire-induced mortality of nearly 100 of the plot species. Our approach allowed us to explore whether various groups of species differed in their susceptibility

to fire-induced mortality and the potential consequences of changing fire regimes. Specifically, we focused on the primary forest type that a tree species was associated with and the canopy status of the tree species. In these seasonal tropical landscapes, evergreen and deciduous forest types occur in mosaic fashion across the landscape. We hypothesised that species that are common in the evergreen forest, but not the deciduous forest would likely be more sensitive to fire. We also expected that understorey species associated with shady, moist environments would be more susceptible to fire-induced mortality than other larger-statured trees. Our approach should facilitate empirical comparisons of the impacts of different fires occurring at the same site, as well as comparisons of species susceptibility and community responses to fires that occur at different sites and in different regions. The broad objective of our study was to understand how fire impacts a species-rich seasonal tropical forest community. To do this, we addressed four specific questions:

1. How did fire intensity vary spatially?
2. How does sensitivity to fire-induced mortality vary among tree species?
3. How do species differ in the minimum size and age above which they are safe from fire-induced mortality (*i.e.*, the “escape size” and “passage time”)?
4. How does the risk exposure associated with shortening fire return intervals vary amongst species by canopy status or forest type association?

Materials and methods

Study area and datasets

The study area is located in the Huai Kha Khaeng Wildlife Sanctuary (HKK) in Uthai Thani Province in western Thailand. HKK is part of the Western Forest Complex, the largest area of protected native forest in continental Southeast Asia. The HKK landscape is dominated by three forest types—seasonal evergreen forest, mixed deciduous forest, and deciduous dipterocarp forest—that co-occur in a complex mosaic. The seasonal evergreen forest is the tallest, most species-rich of the forest types, while the deciduous dipterocarp forest is the least diverse and is associated with poor lateritic soils across the region (Bunyavejchewin *et al.*, 2011, Nguyen and Baker, 2017). The mixed deciduous forest is intermediate in both species richness and forest stature. These forest types have historically been distinguished by the proportion of deciduous species and the degree to which grass or bamboo occur (Bunyavejchewin *et al.*, 2011, Champion and Seth, 1968, Nguyen and Baker, 2017). The deciduous forest types are more prone to fire. During the dry season (Dec-April) they experience large inputs of fine fuels from fallen leaves, which are rapidly dried by the high levels of sunlight reaching the forest floor. The high loads of fine litter, as well as grasses and bamboos, create a highly flammable fuel bed across large areas of the landscape mosaic. In contrast, the evergreen forest type, which maintains most of its canopy cover during the dry season, has much lighter fuel loads and maintains relatively cool, moist microclimatic conditions on the forest floor. Consequently, within these landscapes fires do not burn into seasonal evergreen forests in most years. However, during years of extreme drought, often associated with strong ENSO events, the evergreen canopy species may drop some or all of their leaves leading to greater penetration of sunlight, higher temperatures and lower humidity on the forest floor, and greater fine-fuel biomass (Baker and Bunyavejchewin,

2017, Baker *et al.*, 2008). Under these conditions fire may enter into the seasonal evergreen forest and, in some cases, burn tens of thousands of hectares of the forest type (Baker and Bunyavejchewin, 2009).

We conducted our study in a large (50-ha), long-term forest dynamics plot located in an area of seasonal evergreen forest. The HKK plot is part of the Smithsonian Institution's Center of Tropical Forest Science – Forest Global Earth Observatory (ForestGEO) global forest research plot network. The network comprises over 60 forest research plots across the Americas, Africa, Asia, and Europe, with a strong focus on tropical regions, that collectively monitor the growth and survival of approximately 6 million trees from 10,000 species (<http://www.forestgeo.si.edu>). The HKK plot was initiated in 1991 and the first census was completed in 1994. In each census every living individual tree ≥ 1 cm diameter at breast height (DBH, measured at 1.3 m height) is mapped to the plot coordinates, measured for DBH, and identified to species. The plot is recensused every five years and has been recensused four times (1999, 2004, 2009, 2014). In each recensuse the status (alive or dead) is recorded for each individual that was alive in the previous census and new recruits are mapped, measured, and identified. The HKK plot includes ~ 90000 trees from ~ 300 species. Bunyavejchewin *et al.* (2009) provide a general description of the HKK plot.

Fires have burned through some or all of the 50-ha plot three times since 1991. The first fire occurred in 1992 and burned several hectares in the southwestern corner of the plot. The second fire occurred in 1998 and was associated with the extreme 1997-98 ENSO event in which ~ 1600 km² of HKK burned, including $>95\%$ of the 50-ha plot. The third fire—the subject of this study—occurred in 2005 and burned approximately 2/3 of the plot. Fire in the seasonal evergreen forest is typically low intensity and slow-moving with flame lengths <20 cm and rates of spread <0.015 m/sec (Baker and Bunyavejchewin, 2009). Immediately after the 2005 fire CTFS-ForestGEO Thailand staff conducted a hectare-by-hectare assessment of the fire boundary within the plot (Figure 1b). To estimate the impacts and extent of the 2005 fire on the tree species in the 50-ha plot, we used the 2004 and 2009 census data. We restricted our analyses to trees <30 cm DBH because the fire, due to its low intensity, primarily impacts small trees. To estimate species-specific parameters with enough precision, we only included those species with at least 50 individuals and a DBH range of >10 cm. This resulted in a dataset containing 83851 trees from 93 species in the pre-fire census (2004). In the subsequent 2009 census, 18481 of these trees were determined to be dead. For each of the species in our dataset we assigned a primary forest type that the species is associated with based on the forest type where the species is most often found within the broader HKK landscape and on the known ecology of the species within the region. For brevity, we refer to this as the forest type of the species, which includes seasonal evergreen forest (SEF), mixed deciduous forest (MEF), or in the case of species common to both forest types (both).

We also assigned each species to a canopy status class based on our familiarity with the species across Thailand and, more broadly, continental Southeast Asia. These were canopy, midstorey, understorey, or gap. We distinguished gap species because the assemblage of extreme pioneers in these forests varies widely in adult stature (5-50m), but is a readily identified group within the regional flora. We made our determinations of primary forest type association and canopy status class of each species based on current expert knowledge and our collective 80 years of experience in these forests. We provide species codes and species-specific summary statistics in the supplementary material (Table S2).

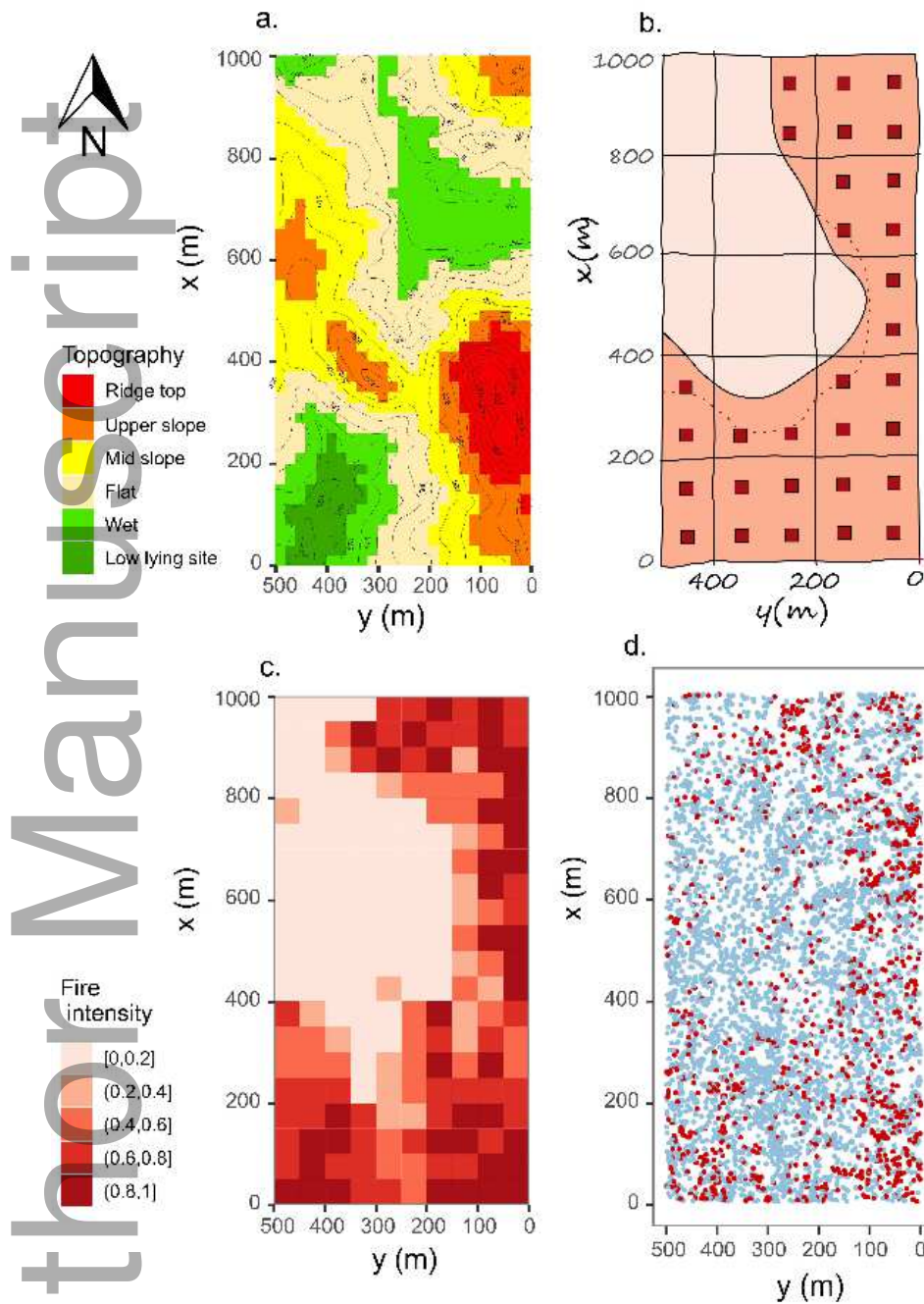


Figure 1: a. Topography of the 50 ha plot. Contour lines show elevation (in meters above sea level). b. Fire extent measured on the ground. Red squares show the center of 1-ha quadrats that were recorded as burnt in 2005 (note: The fire boundaries were hand drawn). c. Fire intensity map estimated from Equation 1. Estimated fire intensity per quadrat is available in Table S1 and Fig.S2 in supplementary materials. d. The location and mortality status of all *Dimocarpus longan* (DIMOLO) at the end of the 2004-2009 census period. Note that x and y-axis are switched as field measures originated from the southeast corner of the plot.

Modelling background and fire-induced mortality

We used a hierarchical survival approach to build a mortality model that simultaneously estimates and separates the effect of background and fire-induced mortality. Conceptually, the survival approach answers two questions: what is the probability that a tree survived the 2005 fire? and if it did, what is the probability that it survived the background mortality until 2009? Each component of mortality was modelled as a hierarchical logistic regression, the product of both survival equations predicting tree survival (and hence tree mortality, see Equation 1). As both background and fire-related mortality were expected to be size-dependent (Brando *et al.*, 2011, Ford, 1975), we included DBH in both components of mortality. Since fire intensity per quadrat was not directly measured in the field, we modelled it as a latent (*i.e.*, unobserved) random variable distributed between 0 and 1 (disturbance intensity was estimated on a relative scale, cf. Canham *et al.*, 2001, 2010). Furthermore, as some quadrats had fire, while others did not, we used a finite mixture approach to separate the estimation of fire intensity on quadrats that had a fire from the estimation of fire intensity on quadrats that did not.

The model is defined as:

$$\begin{aligned}
 dead_{ijk} &\sim \text{Bernoulli}(p_{dead_{ijk}}) & (1) \\
 p_{dead_{ijk}} &= 1 - (1 - p_{background_{ik}}) \times (1 - p_{fire_{ijk}}) \\
 p_{background_{ik}} &= \frac{1}{1 + \exp\left(-(\beta_{1,k} + \beta_{2,k} \cdot \log(DBH_i))\right)} \\
 p_{fire_{ijk}} &= FireInt_j \times \frac{1}{1 + \exp\left(-(\beta_{3,k} + \beta_{4,k} \cdot \log(DBH_i))\right)} \\
 FireInt_j &= ProbFire_j \times FireIntWhenFire_j
 \end{aligned}$$

where DBH_i , $p_{dead_{ijk}}$, and $dead_{ijk}$ are the DBH (in cm), the predicted probability of mortality during the 5-year intercensal interval, and the 2009 mortality status (0=alive, 1=dead) of tree i , in quadrat j , of species k . We used $\log(DBH)$ instead of DBH as it allowed for a steeper initial slope of the p_{dead} -DBH relationship and provided a better fit to the data (not shown). We estimated the pooled parameters β and σ_β , as well as the species-specific parameters β_k for species k . We used β_1 and β_2 to represent the size-independent and size-dependent background mortality, respectively, and β_3 and β_4 to represent the size-independent and size-dependent fire-induced mortality, respectively. $FireInt_j$ is the latent variable representing the fire intensity in quadrat j , which was itself modelled as a mixture of two processes: the presence of fire in the quadrat ($ProbFire_j$) and the fire intensity in the quadrat conditional on the fire being present ($FireIntWhenFire_j$). Since the probabilistic language that we used (Stan, 2016) does not allow for discrete parameters, we had to marginalize $FireInt_j$ as a product of $ProbFire_j$ and $FireIntWhenFire_j$ (see Eq. 1).

$$\begin{aligned}
 ProbFire_j &\sim \text{Beta}(s_1, s_2) & (2) \\
 FireIntWhenFire_j &\sim \text{Beta}(3, 1.5)
 \end{aligned}$$

To better separate quadrats that burnt from quadrats that did not, we wanted $ProbFire_j$ to take values either close to zero or to one. We implemented this idea by sampling $ProbFire_j$ from a Beta distribution with a particularly high intra-cluster correlation coefficient (ICC = 0.99). We

estimated the proportion of quadrats that burnt ($\overline{ProbFire}$) directly from the data with a non-informative hyperprior (*i.e.*, $ProbFire \sim Beta(2, 2)$ with 95% CI in the 0.09–0.91 range). As the Beta distribution in Stan is not parametrized by its mean and ICC but by its shape parameters s_1 and s_2 , we re-parametrized $ProbFire_j$ in the transformed parameter block of the Stan model ($s_1 = \overline{ProbFire}/ICC - \overline{ProbFire}$ and $s_2 = \overline{ProbFire}(1 - 1/ICC) + 1/ICC - 1$). To explore variability in fire intensity for quadrats that burnt, we used a Beta(3, 1.5) prior for $FireIntWhenFire_j$ (*i.e.*, 95% CI in the 0.23–0.97 range), which essentially spreads the distribution across a large range of relative fire intensity values, but avoids values that are too low, which would cause identifiability issues. The prior distributions for $ProbFire_j$ and $FireIntWhenFire_j$, as well as the distribution of $FireInt_j$ that result from their combination, are shown in the supplementary material (Fig. S1).

The estimated species random effects were distributed as:

$$\begin{aligned}\beta_{1,k} &\sim N(\beta_1, \sigma_{\beta_1}) \\ \beta_{2,k} &\sim N(\beta_2, \sigma_{\beta_2}) \\ \beta_{3,k} &\sim N(\beta_3, \sigma_{\beta_3}) \\ \beta_{4,k} &\sim N(\beta_4, \sigma_{\beta_4})\end{aligned}\tag{3}$$

where species-specific parameters were modelled as the sum of a statistical population term, plus a species-specific deviation from this population term (*i.e.*, random coefficient) sampled from a Gaussian distribution with a mean of zero and standard deviation to be estimated. The partial pooling of information among species allows for better estimates of parameter values and uncertainties for rare species (Gelman and Hill, 2007) and is particularly relevant for species-rich tropical forests where local abundance can vary by several orders of magnitude. Stan code for the hierarchical model can be found in section S2 of supplementary materials.

Validating latent fire intensity estimates

The reliability of our modelling method depends on getting reasonable estimates for the unobserved fire intensity in different parts of the 50-ha plot. We validated spatial patterns of relative fire intensity estimated from our model against a map of the fire boundary developed by the field staff in the days after the fire. It is important to note that we reconstructed fire occurrence and intensity on a 0.25 ha basis (*i.e.*, 50×50 m), which is finer resolution than the field survey of fire extent, which was on a per hectare basis. We used 0.25 ha quadrats for our estimation because they provided a reasonable balance between spatial resolution of fire intensity estimates and sufficient sample sizes for robust parameter estimation.

Ranking and classifying species-specific susceptibility to fire-induced mortality

To better understand how changing fire regimes may impact the forest structure and composition, we estimated the size at which an individual of a given species had a 50% probability of surviving a fire and the amount of time required to reach this threshold size. To do this required three steps: 1) calculating the *DBH* at which a species has a 50% probability of surviving a fire (we refer to this as as species' $DBH_{50\%}$); 2) calculating the growth rate of median- and fast-growing individuals for each species (ΔDBH , in $cm\ year^{-1}$); and 3) computing the amount of time required to reach the fire-safe threshold size (*i.e.*, the ratio of $DBH_{50\%}$ to ΔDBH , in years).

Species-specific fire-safe size thresholds

We calculated $DBH_{50\%}$ for each species k by setting $p_i = 0.5$ and $FireInt_j = 1$ in the fire-induced mortality part ($p_{fire_{ijk}}$) of Eq. 1 and then solved for DBH . This gives:

$$DBH_{50\%,k} = \exp\left(-\frac{\beta_{3,k}}{\beta_{4,k}}\right) \quad (4)$$

We then ranked each species based on their $DBH_{50\%}$ values. Fire-resistant species have low $DBH_{50\%}$ values—that is, even small stems have a 50% probability of surviving the most intense fire observed. In contrast, fire-sensitive species have high $DBH_{50\%}$ values—that is, only large individuals have a 50% chance of surviving an intense fire. For our analyses, we limited $DBH_{50\%}$ estimates to the studied DBH range (1-30 cm). We filtered one species (*Senna timorensis*, SENNTI, a fast-growing, short-lived tree) from these analyses as the uncertainty interval for $\beta_{4,k}$ (95% CI -1.89–0.28) was too large and overlapped with zero, leading to unstable $DBH_{50\%}$ values. For this species, 7% of the posterior mass of $\beta_{4,k}$ was positive and we cannot rule out that larger individuals are more sensitive to fire than smaller individuals.

Species-specific growth rates and the length of risk exposure

For each species, we computed the median and 95th percentile annual diameter growth rates (ΔDBH , in cm year^{-1}). These represent the growth of average and fast-growing individuals, respectively. To avoid including the effect of fire on tree growth, we calibrated these growth rates from the 1999-2004 period (which had no fire) instead of the 2004-2009 period (ΔDBH in the 2004-2009 period was on average 0.93 times lower than in the 1999-2004 period, suggesting detrimental effects of fire on tree growth, see Fig. S4 in supplementary materials).

The time required to reach the fire-safe threshold size was then computed as the ratio of $DBH_{50\%}$ to ΔDBH (age to $DBH_{50\%}$, in years). Since we had no data for tree growth below 1 cm, but this estimate was necessary to compute the age at $DBH_{50\%}$, we had to assume tree growth below 1 cm to be similar to tree growth above 1 cm. While this assumption is plausible (we found no evidence of an effect of DBH on ΔDBH for trees in the 1–10 cm DBH range, not shown) and is unlikely to affect the ranking of species sensitivity to fire (species that are slow growing > 1 cm DBH are unlikely to be fast growing species < 1 cm and vice-versa), our method only provides approximations to the age required to reach $DBH_{50\%}$. Data on growth rates from seedling establishment to 1 cm DBH would be needed to get exact estimates of the age to $DBH_{50\%}$. Due to this assumption, age to $DBH_{50\%}$ values obtained in this paper should be interpreted cautiously.

Relating $DBH_{50\%}$, ΔDBH , and age to $DBH_{50\%}$ to forest type and canopy status

We used hierarchical linear models to predict $DBH_{50\%}$, ΔDBH , and age to $DBH_{50\%}$ values for any combination of forest type (*i.e.*, seasonal evergreen, mixed deciduous, both, or unknown) and canopy status (*i.e.*, canopy, midstorey, understorey, and gap species). As ΔDBH and age to $DBH_{50\%}$ were log-normally distributed, ΔDBH and age to $DBH_{50\%}$ were log-transformed

before model fitting. The models is described as:

$$\begin{aligned}
 y_{ijk} &= \alpha_0 + \alpha_j \times FT_j + \alpha_k \times CS_k + \alpha_{jk} \times FT_j \times CS_k + \varepsilon_i \\
 \alpha_j &\sim N(0, \sigma_{ft}) \\
 \alpha_k &\sim N(0, \sigma_{cs}) \\
 \alpha_{jk} &\sim N(0, \sigma_{ft,cs}) \\
 \varepsilon_i &\sim N(0, \sigma)
 \end{aligned}
 \tag{5}$$

where y_{ijk} is the observed response value ($DBH_{50\%}$, $\log(\Delta DBH)$ or $\log(\text{age to } DBH_{50\%})$) for species i , in forest type (FT) j , and canopy status (CS) k . α_0 , σ_{ft} , σ_{cs} , $\sigma_{ft,cs}$, and σ are population parameters and ε_i are residuals. Equation 5 predicts the mean response value and associated uncertainties for each combination of forest type and canopy status.

Parameter estimation procedures

All data management and analyses were conducted using the statistical computing software R (R, 2015). The latent fire intensity and tree mortality model (Equation 1) was fitted using Rstan (Stan, 2016). We used weakly informative priors to help convergence (Gelman, 2006). Gaussian distributions (mean=0, sd=5) were used for the β parameters and half-Gaussian distributions (mean=0.5, sd=1) for the standard deviation parameters σ of the mortality model (Equation 1). These priors on the parameters are relatively flat in the range of interest and should not affect our posterior estimates, which range from -2.5 to 2.3 for the β and 0.6–1 for the σ parameters of the mortality model (Table 1). We used the ‘stan_glmmer’ function from the ‘rstanarm’ package (Goodrich *et al.*, 2018) to relate $DBH_{50\%}$, ΔDBH , and age to $DBH_{50\%}$ to forest type, canopy status, and their interaction (Equation 5). For these models, we used ‘stan_glmmer’ with default priors and the ‘autoscale = TRUE’ argument. The default prior for the intercept terms is a Gaussian(mean=0 and sd=10) distribution. The default prior for the standard deviation of the random effect is an exponential distribution with a mean of one. However, since we used the ‘autoscale = TRUE’ argument, the scale of the default priors (SD of the Gaussian, mean for the exponential distribution) are adjusted by multiplying them by the standard deviation of the response variable (*e.g.*, for the $DBH_{50\%}$ model, the SD of the response was 2.14 so that the effective SD of the Gaussian distribution prior on the intercept was 21.4 and the effective mean for the exponential distribution prior on the standard deviation of the random effects was 2.14). Markov chains were visually checked to inspect sampling behaviour and convergence; however, no issues were detected.

Results

Our model-derived estimates of fire intensity identify an area in the centre and northwest of the plot that did not burn or only experienced very low-intensity fire (Figure 1c). These results align extremely well with the observed fire boundaries that were recorded in the 50-ha plot immediately after the 2005 fire occurred (Figure 1b). This is important because the model-derived spatial patterns of fire intensity emerge from the observed patterns of survival and mortality across many species and size classes rather than direct observations of fire or fire effects (*e.g.*, char height, residual twig diameter). Figure 1d provides an example of the observed mortality of one species, *Dimocarpus longan* (DIMOLO; Sapindaceae), a common midstorey tree throughout the plot, showing the relationship between mortality patterns and fire intensity.

Table 1: Mean and 95% credible intervals for population-level parameters of the size-dependent background and fire-mortality model (Equation 1). Species-specific parameters are provided in the supplementary materials (Table S2).

Parameter	Description	Mean	95% CI	
			Min	Max
β_1	Intercept of background mortality	-1.88	-2.18	-1.59
β_2	Slope of log(DBH) on background mortality	-0.45	-0.61	-0.28
β_3	Intercept of fire-induced mortality	2.26	1.98	2.54
β_4	Slope of log(DBH) on fire-induced mortality	-2.54	-2.83	-2.29
σ_{β_1}	Random effect SD for β_1	1.01	0.81	1.25
σ_{β_2}	Random effect SD for β_2	0.62	0.5	0.77
σ_{β_3}	Random effect SD for β_3	0.86	0.65	1.13
σ_{β_4}	Random effect SD for β_4	0.78	0.59	0.99
$DBH_{50\%}$	Mean DBH at which 50% of trees survive a fire	2.45	2.22	2.73
$ProbFire$	Proportion of burnt quadrats in the 50 ha plot	0.5	0.46	0.55

Our modelling approach provided estimates of both background and fire-induced mortality (see Equation 1). The population (*i.e.*, pooled across species) parameter estimates for the model are given in Table 1. When all species are pooled together, the estimate of the probability of background mortality of a tree of 1 cm DBH is 13% over the census period. However, when fire-induced mortality is included and set to one, the mortality rate increases to 92%. Figure 2 highlights the large increase in fire-induced mortality (over background mortality) for several tree species in the HKK plot. The probability of fire-induced mortality is much higher for the smallest trees in each of the species in Figure 2. However, these four species also illustrate the interspecific variability in the effect of size on fire-induced mortality. In *Macaranga siamensis* (MACASI; Euphorbiaceae), a fast-growing, gap-phase pioneer, the probability of fire-induced mortality is significantly higher (*i.e.*, 95% CIs do not overlap) than background mortality for trees as large as 20 cm DBH. In contrast, *Dimocarpus longan* shows no significant differences in fire-induced and background mortality above 6 cm DBH. The other two species, *Aglaia spectabilis* (AGLASP; Meliaceae) and *Milium horsfieldii* (SACCLI¹; Annonaceae) are intermediate in terms of the maximum size at which fire-induced mortality remains significantly higher than background mortality. Species-specific parameter estimates for the mortality model parameters are available in supplementary materials (Table S2).

To compare interspecific differences in sensitivity to fire, we ranked $DBH_{50\%}$ for all species included in the analyses. The four species that were identified as gap-dependent species (*i.e.*, pioneers, only found in the seasonal evergreen forest type in our dataset) had significantly higher $DBH_{50\%}$ values than canopy, midstorey, and understorey species (Figures 3 and 4). That is, the size that individuals had to reach before the probability of mortality and survival were equivalent was much larger for gap species than it was for the non-gap species. When we compared the $DBH_{50\%}$ across forest-type associations, we found that tree species associated primarily with the seasonal evergreen forest (SEF) had slightly larger $DBH_{50\%}$ values than species associated with either mixed deciduous forest (MDF) or both forest types. However, there was

¹*Milium horsfieldii* was originally called *Saccopetalum lineatum* in the database. We kept the acronym SACCLI in this paper as it is the current species identifier used in the CTFS-ForestGEO database

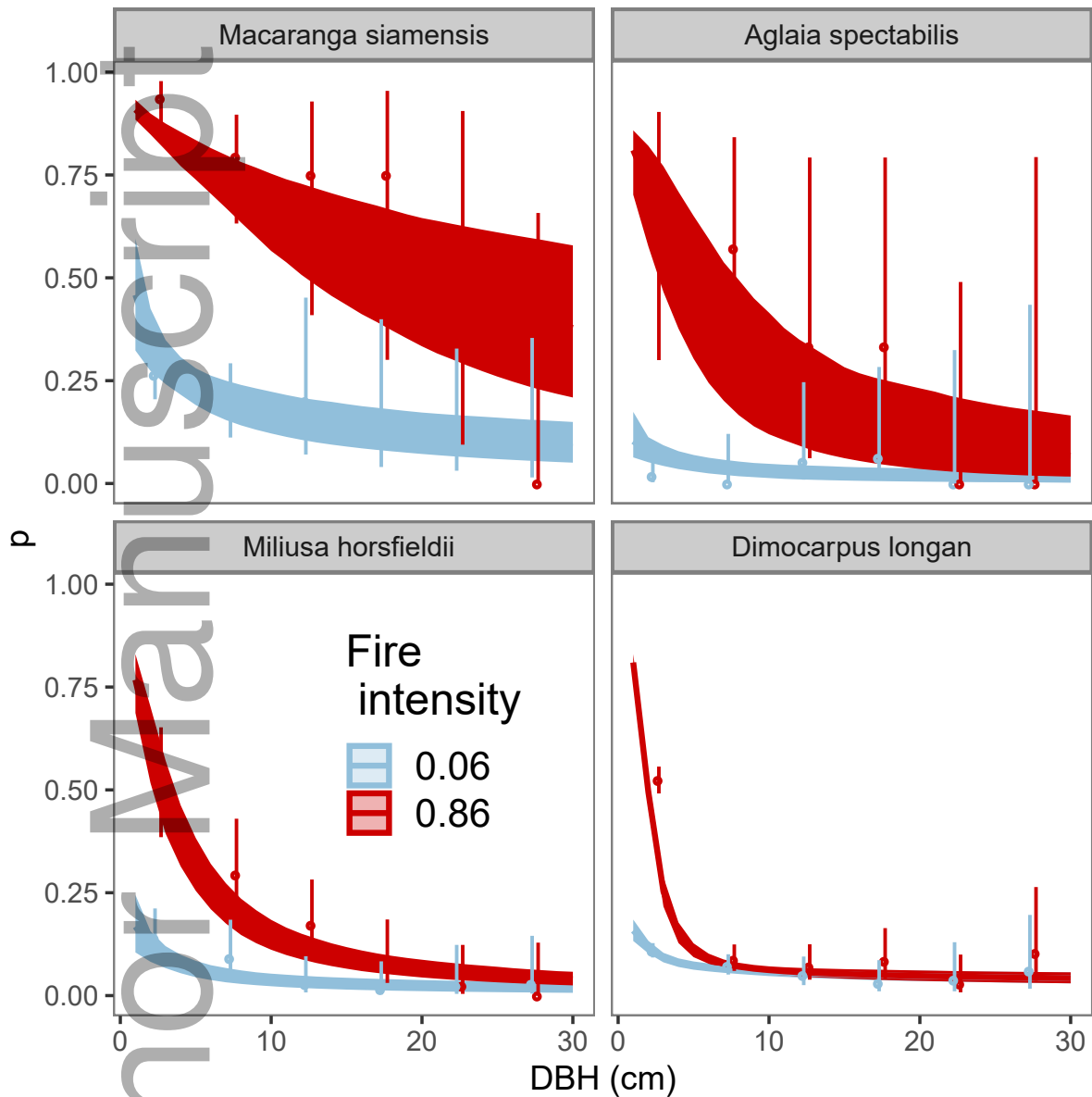


Figure 2: Effect of *DBH* and *FireInt* on tree mortality for four species varying in their fire sensitivity (plots for all 93 species are available in Fig. S5 of the supplementary materials). Dots represent the proportion of individuals that died in the 2004–2009 period split by *DBH* and *FireInt* classes. The low *FireInt* class contains observed mortality data from quadrats that had an estimated *FireInt* < 0.25 (mean *FireInt* = 0.06) while the high *FireInt* class contains observed mortality data from quadrats that had an estimated *FireInt* > 0.75 (mean *FireInt* = 0.86). 95% Wilson binomial CI (Brown *et al.*, 2001) are shown for observations. Lines and shadows are mean and 95% CI model predictions, respectively.

Table 2: Parameter values and predictions (on the original scale) of $DBH_{50\%}$, ΔDBH , and age at $DBH_{50\%}$ for each combination of forest type and canopy status (Equation 5). Species-specific parameters are provided in the supplementary materials (Table S3).

	$DBH_{50\%}$		ΔDBH				age at $DBH_{50\%}$			
			Median		Fast		Median		Fast	
	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
α_0	4.07	1.79	-1.66	0.38	-0.40	0.28	2.68	0.27	1.40	0.28
σ	1.73	0.13	0.51	0.04	0.37	0.03	0.54	0.04	0.44	0.04
σ_{ft}	0.95	1.58	0.26	0.42	0.22	0.36	0.35	0.52	0.36	0.53
σ_{cs}	3.41	3.16	0.57	0.73	0.48	0.57	0.37	0.99	0.24	0.33
$\sigma_{ft,cs}$	0.61	0.98	0.37	0.41	0.32	0.33	0.32	0.32	0.28	0.28
$\alpha_{SEF,Und}$	2.70	0.46	0.09	0.01	0.34	0.04	25.95	4.43	7.24	1.01
$\alpha_{SEF,Mid}$	2.99	0.29	0.18	0.02	0.63	0.04	16.63	1.58	4.70	0.36
$\alpha_{SEF,Can}$	2.69	0.39	0.18	0.02	0.66	0.06	14.32	1.88	3.82	0.43
$\alpha_{SEF,Gap}$	9.25	1.05	0.42	0.14	1.37	0.31	15.29	3.91	4.71	1.01
$\alpha_{MDF,Und}$	2.35	0.73	0.17	0.07	0.63	0.19	12.09	4.23	3.25	1.00
$\alpha_{MDF,Mid}$	2.54	0.57	0.14	0.03	0.59	0.09	15.73	3.50	3.65	0.68
$\alpha_{MDF,Can}$	2.62	0.49	0.18	0.03	0.72	0.09	13.88	2.40	3.55	0.53
$\alpha_{Both,Und}$	2.15	0.80	0.13	0.05	0.42	0.12	14.46	5.00	4.21	1.26
$\alpha_{Both,Mid}$	2.28	0.52	0.16	0.03	0.56	0.07	12.31	2.10	3.54	0.49
$\alpha_{Both,Can}$	2.22	0.49	0.18	0.03	0.72	0.09	12.01	2.07	2.99	0.41

some overlap in the forest-type parameter distributions for $DBH_{50\%}$ (Table 2). Analyses of the plot census data showed that growth rates varied widely within and among species. The fastest-growing species group (gap species, median growth rate = 0.33 cm year⁻¹) grew approximately three times faster than the slowest-growing species group (understorey species of the seasonal evergreen forests type, median growth rate = 0.1 cm year⁻¹). However, there was also considerable variability in ΔDBH among species (Fig. 4). On average, the fast-growing individuals (95th-percentile ΔDBH) across all species grew approximately three times faster (0.43 cm year⁻¹) than individuals growing at the median growth rate (0.14 cm year⁻¹). This has important consequences for the age at which individuals of different species reach their fire-safe size threshold, as both $DBH_{50\%}$ and diameter increment contribute to the amount of time required to reach $DBH_{50\%}$. The average time required for fast-growing individuals across all species to reach their $DBH_{50\%}$ was 5 years; for median growth rates it took 17 years on average to reach this size (Figure 4). While the gap species were the most fire sensitive (*i.e.*, they had the largest $DBH_{50\%}$), their rapid growth rates meant that the time required to reach that size was similar to the other groups (5 and 18 years for fast- and median-growing individuals, respectively). In contrast, the understorey species associated with the seasonal evergreen forest had a modest $DBH_{50\%}$ (mean across species = 2.7 cm), but their slow growth rates meant that they required more time than any other group to reach $DBH_{50\%}$ (8 and 30 years for fast- and median-growing individuals, respectively). The most extreme case was *Micromelum minutum*, an understorey species from the seasonal evergreen forest, that requires 36 years for fast-growing individuals and up to 190 years for median-growing individuals (~ 7 –11 times longer than average) to reach a $DBH_{50\%}$ of 5.1 cm. Species-specific parameter estimates for $DBH_{50\%}$, ΔDBH , and age at which $DBH_{50\%}$ is reached are available in supplementary materials (Table S3).

Discussion

In the temperate zone the low diversity of the forest communities combined with more than a century of direct observations and decades of dendroecological studies have contributed to a detailed understanding of how disturbances shape the structure, composition, and dynamics of forests (Oliver and Larson, 1996). Tropical forests, in contrast, are extremely diverse, have relatively short histories of observation, and few tree species with annual growth rings for dendroecological analyses. This has severely constrained even the most basic understanding of the role of fire disturbances on tropical forests (Baker *et al.*, 2005, Zuidema *et al.*, 2013). In this study we used direct observations of mortality in a large-scale, long-term forest dynamics plot that experienced a fire to estimate both fine-grained spatial variability in disturbance intensity and species-specific differences in susceptibility to fire. We then calculated interspecific differences in the length of exposure to risk of fire-induced mortality within the forest community. These analyses provide new insights into the nature of fire in seasonal tropical environments, community-level variability in terms of susceptibility to fire, and the potential consequences of changing fire regimes on the composition and structure of these forests.

Variability in disturbance intensity

Direct observations of disturbance intensity in forests are rare. Post-disturbance observations are complicated by the susceptibility of a forest to the disturbance. Species within the forest may vary widely in their ability to withstand a disturbance and these differences may vary as a function of tree size. For example, a disturbance of a given intensity may have very different impacts on two forest stands if one stand is composed of small individuals of a species and the other is composed of large individuals of a species. Similarly, if one stand is composed of species susceptible to the disturbance and the other is composed of species resistant to the disturbance, there may be very different outcomes in terms of mortality despite the *intensity* of the disturbance being uniform. This problem is particularly acute in tropical forests due to the high levels of species richness and complex size structures of these forests.

To estimate unobserved disturbance intensities Papaik and Canham (2006) and Canham *et al.* (2010) developed a statistical approach using only observed mortality patterns in temporary forest inventory plots established after hurricanes in the northeastern USA and Puerto Rico, respectively. Their approach successfully generated site-specific estimates of disturbance intensity and species-specific estimates of susceptibility to mortality. It is also relatively easy to implement—it simply requires the establishment of a temporary network of small plots across the gradient of disturbance severity shortly after the disturbance to ensure that the only source of observed mortality is from the disturbance of interest. Over the past 30 years there has been a rapid growth in the number of large-scale, long-term forest dynamics plots around the world. Due to their large size, high stem densities, and remote locations, it is often impossible to rapidly recensus them immediately after a disturbance. Subsequent censuses then will include both disturbance-mediated mortality and background mortality. Our approach extends that of Papaik and Canham (2006) to census data from long-term forest plots in which mortality is only observed at fixed, superannual intervals. This requires partitioning the direct impacts of the disturbance from the background mortality that occurs during the intercensus interval. A comparison of the estimated fire intensity across 200 0.25 ha quadrats within the HKK forest dynamics plot and field observations of the fire boundaries conducted within days of the fire passing showed remarkably consistent patterns. We found that the southern part of the 50 ha

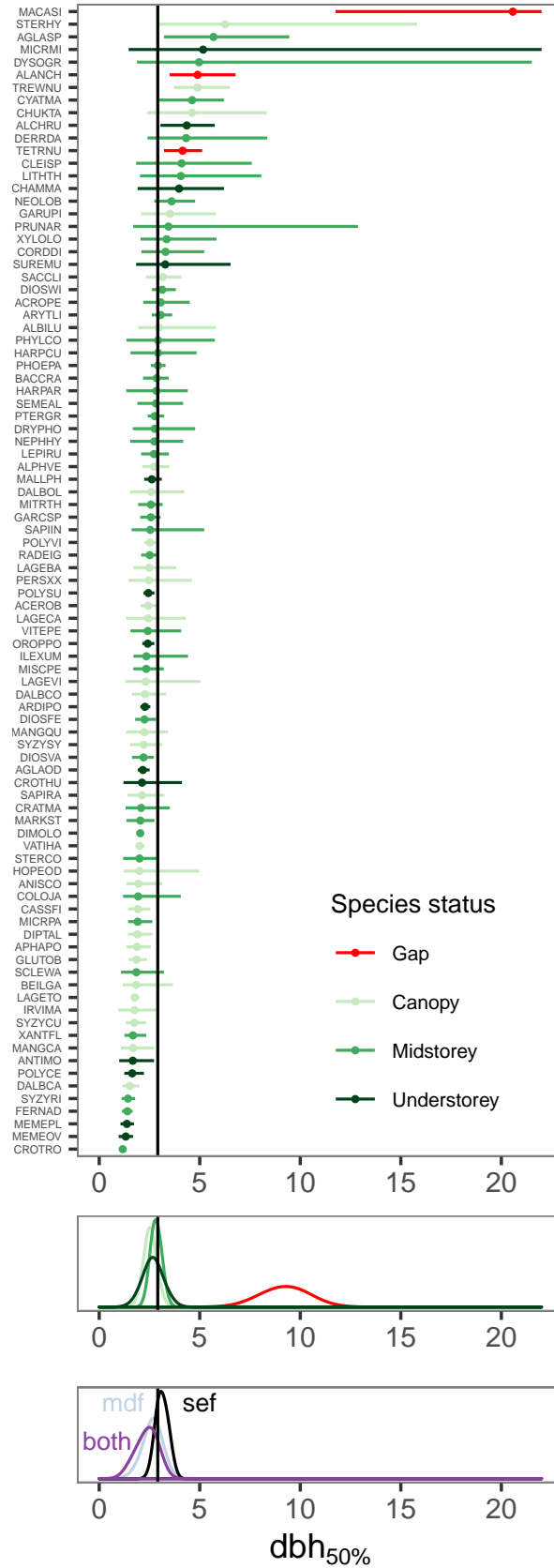


Figure 3: Estimated $DBH_{50\%}$ for species pooled by canopy status category and forest type association are shown below the graph. The upper and middle panels highlight the much larger $DBH_{50\%}$ values of gaps species compared to the other groups and the lack of differences among the other groups. The lower panel suggests that species who are associated with seasonal evergreen forest (SEF) have slightly larger $DBH_{50\%}$ values than species associated with mixed deciduous forest (MDF) or both forest types.

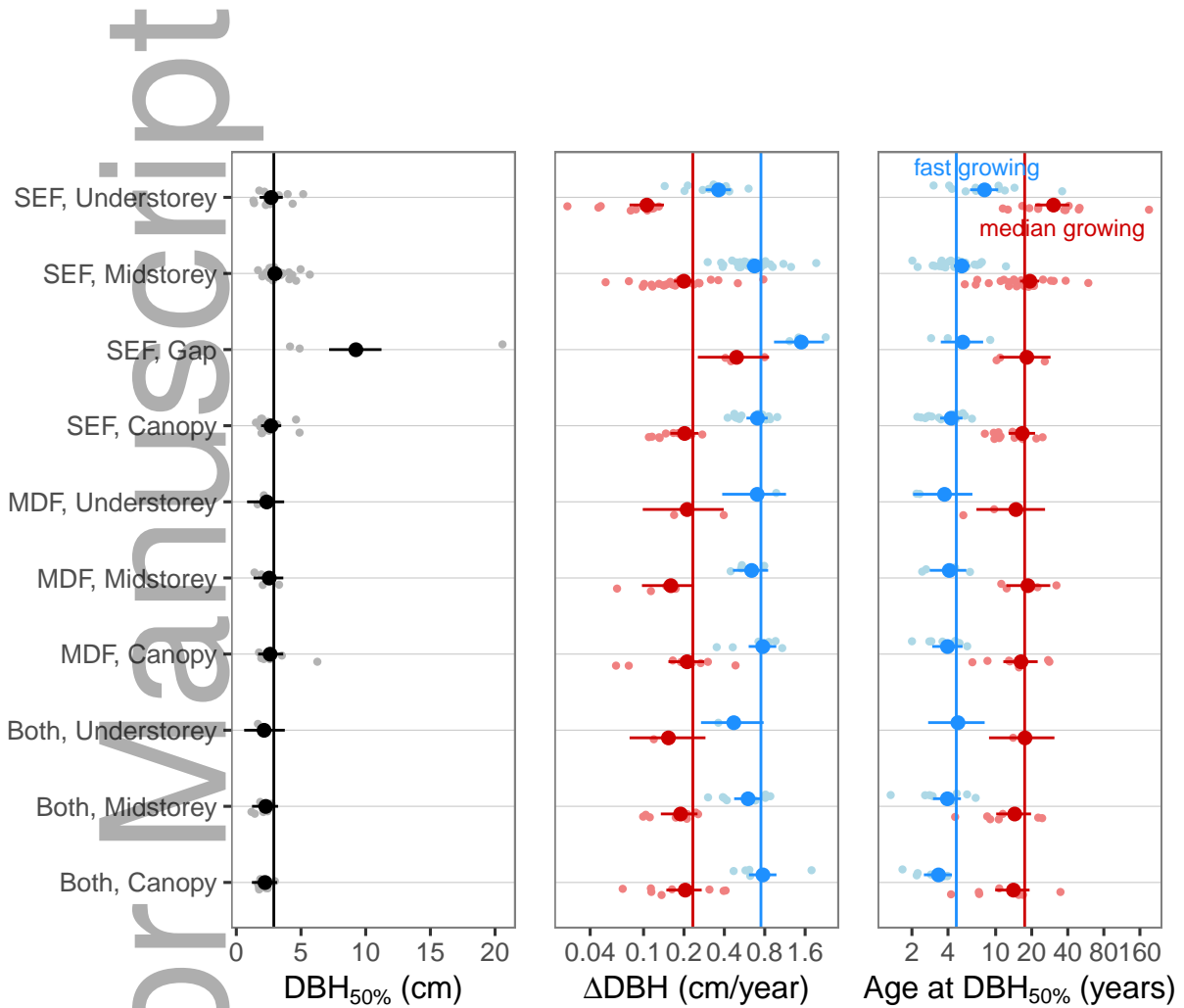


Figure 4: Variations in $DBH_{50\%}$, ΔDBH , and age at which $DBH_{50\%}$ is reached ($\frac{DBH_{50\%}}{\Delta DBH}$) associated with forest type and canopy status. To highlight how individual variation in DBH growth within a species can affect the age at $DBH_{50\%}$, we show our results for both fast-growing individuals (95th percentile growth for the species, in black) and average growing individuals (median growth for the species, in red). Note that the x-axis is on a linear scale for the left-hand panel and a log scale for the middle and right-hand panels.

plot was completely burned (Fig. 1c.), with the extreme southwest and southeast corners experiencing the most intense fire. The northwestern and central portions of the plot experienced no fire or very little fire and the northeastern corner was the most variable. While the estimates of fire intensity are relative (*i.e.*, not an absolute measure of fire-line intensity) and scaled from no observed fire ($I=0$) to the most intense fire observed ($I=1$), they provide useful insights into local variability of fire intensity. Direct observations of fire in these forests during the 1997-98 ENSO event found that although the fires were of low intensity with flame lengths generally <20 cm (and rarely greater than 50 cm), there was notable variability in fire impacts among the three dominant forest types in the HKK landscape (Baker and Bunyavejchewin, 2009, Baker *et al.*, 2008). However, these observations were based on indirect estimates of fire intensity such as scorch height and the size of gaps created by the fire. Given the slow rate of spread of these fires, it may be possible to link relative fire intensity to absolute fire intensity by placing thermocouples or temperature-sensitive paint chips out in front of the slowly advancing fireline in the future.

There are many potential drivers of the observed variation in fire intensity within the HKK plot. These include site and vegetation effects (*e.g.*, canopy cover, species composition), stochastic factors such as weather and fuel dynamics, as well as their potentially complex interactions. For example, in the HKK plot the area that did not burn in the centre of the plot is relatively wet and, in some places, even swampy with a dense undergrowth of Zingiberaceae and other herbaceous species that keep the forest floor cool and moist. Even during the height of the dry season, this area rarely shows evidence of drying out. This part of the 50-ha plot is also notable for the dominance of two emergent dipterocarps, *Hopea odorata* and *Dipterocarpus alatus*, and a relatively dense midstorey of various evergreen Annonaceae, Lauraceae, and Guttiferae. The multi-layered canopy of evergreen species creates considerable shade throughout the year, including during the dry season, keeping temperatures low and humidity high across the forest floor. In contrast, the southern section of the plot, which was completely burned, is dominated by *Lagerstroemia* spp. and *Tetrameles nudiflora*, which are deciduous or semi-deciduous during the dry season. The greater penetration of sunlight to the forest floor allows grasses and weedy perennials to establish and during the dry season to cure and become a flammable fuel bed (Baker and Bunyavejchewin, 2009). However, despite the more flammable conditions in the southern part of the plot, there is little evidence (beyond the 2005 fire) of more frequent fires in this part of the forest. In the dry season of 1992 a fire burned ~ 3 ha in the southwestern-most corner of the plot, but did not spread into other potentially flammable areas adjacent to it (Grogan J., unpublished report). While direct observations of fire behaviour do not exist, post-fire investigations suggest that even under extreme weather conditions (*i.e.*, 1998 ENSO drought), small changes in fuel structure can inhibit the passage of fire (P.J. Baker, personal observation). For example, after the 1998 fire we found that permanent animal trails, which are rarely more than 40 cm wide and either have reduced leaf litter or the leaf litter is compressed from animal trampling, created inadvertent fire breaks. As a consequence, interactions between the direction of fire spread and the spatial arrangement of the complex network of animal trails created occasional patches within the 50-ha plot that did not burn even under the most extreme drought conditions in the past 35 years.

Species-sensitivity to fire

Differences in species-specific susceptibility to disturbances can have significant effects on the observed impacts of a disturbance (Papaik and Canham, 2006). In species-rich tropical forests,

where several hundred species may co-occur, empirical estimates of susceptibility either do not exist or only exist for a handful of the species in a community. Furthermore, given the scale of species richness in tropical forests, sufficient sampling to account for covariates such as tree size, which are often important determinants of mortality, is difficult to accommodate. In this study we were able to estimate size-specific fire susceptibility for 93 sympatric tree species in the HKK plot due to the scale and history of measurements. This provides a rich dataset for examining community-level responses to fire and for developing predictive models of community composition under potential future fire regimes. For example, our analyses allowed us to test for differences in adult stature and forest-type association on fire susceptibility. We hypothesised that species associated with deciduous forest types (*i.e.*, mixed deciduous and deciduous dipterocarp) would be less susceptible to fire-induced mortality (Charles-Dominique *et al.*, 2017, Hoffmann *et al.*, 2003, Schafer *et al.*, 2015). Across continental Southeast Asia the deciduous forest types experience more frequent fires than evergreen forests. As such, tree species associated with the deciduous forest types might be expected to be better adapted to fire with adaptations such as thick bark or rapid height growth (Nguyen *et al.*, 2019). When we compared the posterior estimates of $DBH_{50\%}$ for all species grouped by forest type association, we found that tree species associated with the seasonal evergreen forest had slightly larger $DBH_{50\%}$ values than species associated with the mixed deciduous forest. But these differences were not significant and suggest that there is little evidence for differences in susceptibility amongst the species associated with the different forest types. In contrast, a comparison of canopy status showed that gap species, which in our dataset were limited to the SEF, were much more sensitive to fire than non-gaps species. However, it is important to note that all gap species were from the SEF type.

While size may be an important determinant of survival for a single fire event, long-term persistence under a particular fire regime requires being able to reach a fire-safe size threshold before the next fire occurs. We used our model-derived estimates of $DBH_{50\%}$ and empirical estimates of ΔDBH from the 50-ha plot to calculate the expected time required to reach a fire-safe threshold size for individuals growing at the median and 95th percentile growth rates for each species. We found that the high growth rates of the gap species compensated for their much larger $DBH_{50\%}$ values and allowed them to reach a fire-safe size in the same amount of time as most other species groups. The species most at risk of fire-induced mortality are those with a larger than average $DBH_{50\%}$ and slower than average ΔDBH . These were primarily understorey and midstorey species associated with the SEF. For some of these species, even the fast-growing individuals would require more than 20 years to reach their $DBH_{50\%}$ (Fig. 4). The longer exposure to fire risk of understorey species in the SEF means that their chance of being eliminated from the community is likely to increase with fire frequency, unless they possess other adaptations to frequent fire, such as vigorous basal sprouting (Clarke *et al.*, 2013, Pausas *et al.*, 2016). Replacement of SEF species by MDF species in the understorey of the 50-ha plot could trigger positive feedbacks with the fire regime as the MDF species shed leaves during the dry season, further increasing the dominance of species associated with the deciduous forest types over those from the seasonal evergreen forest. Note that while our paper focuses on growth and mortality of trees >1 cm DBH to estimate species-sensitivity to fire, additional aspects of species demography such as seed dispersal and seedling recruitment might also need to be studied to get a more complete picture of species response to fire in these tropical forests. Fire return intervals in tropical forests are largely unknown. While fire has occurred in continental Southeast Asian landscapes for millennia (Maxwell, 2004, Penny, 2001) and many species

are adapted to fire, changes in fire return intervals have the potential to reshape community composition and the distribution of species across the remaining forested landscapes. At the HKK plot, three fires have occurred within the 50-ha plot since 1991, an average fire return interval of nine years. However, only a small area of the plot experienced all three fires, so the average fire return interval will be considerably longer across most of the plot. In one of the only reconstructions of disturbance history from a tropical forest, Baker *et al.* (2005) working in and around the HKK plot found evidence of four moderate disturbance events during the period 1890-1985. These were consistent with the directly observed mortality patterns associated with the 1998 ENSO-driven fires and imply a fire-return interval over the 20th Century of ~ 23 years. Most species in our study would have some fast-growing individuals capable of reaching their species-specific fire-safe threshold sizes under these conditions. Our results, however, establish a fire frequency threshold (~ 7 years) at which even the fastest-growing individuals of many species would not be able to reach their fire-safe threshold sizes. If fire return intervals were reduced to less than seven years, these species would struggle to persist unless they had other adaptations to frequent fire. It is worth noting that the species that requires the shortest time to reach its fire-safe size threshold is *Croton roxburghii* (1.3 years for fast-growing individuals), the most abundant tree species on the 50-ha plot. After the 1998 fire, the number of *C. roxburghii* in the 50-ha plot nearly tripled (Baker *et al.*, 2008). If fire return intervals decrease in the future, many of the slow-growing understorey species in the SEF may be replaced by *C. roxburghii*, which would greatly reduce the overall species richness and diversity of the SEF.

Predictive modelling of community dynamics

Fire is a significant source of mortality in seasonal tropical forests. Differences among species in their susceptibility to fire-induced mortality mean that changes to fire regimes could shift community composition and dynamics in the future. Developing predictive models of community dynamics under a range of future conditions requires an explicit characterisation of species-specific responses to fire, as well as an understanding of the nature of variability in fire intensity. Our analyses of the 2005 fire that burned through part of the HKK forest dynamics plot provide empirical estimates for both. These can be tested against subsequent fires to explore inter-annual variability in fire dynamics, the consistency of species-specific fire responses across fires, and the potential role of legacy effects in areas that have been burned multiple times. Indeed, a catalogue of spatially explicit fire intensity reconstructions for a single forest would provide unique and valuable insights into the interacting effects of multiple fires on mortality, recruitment, and growth dynamics. These could then provide the foundation for a model of seasonal tropical forest dynamics capable of exploring the potential impacts of climate-change induced shifts in fire regimes on forest community structure and composition. Such a model could be used as input into earth systems models that attempt to characterize the impacts of climate change on regional-scale forest dynamics.

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Authors' contributions

R.T. and P.B. designed the study. S.B. is principal investigator of the 50-ha plot and supervised all data collection and quality control. R.T. analyzed the data and built the models. R.T. and P.B. wrote the first draft. R.T., P.B., and S.B. all contributed to revisions.

Data availability statement

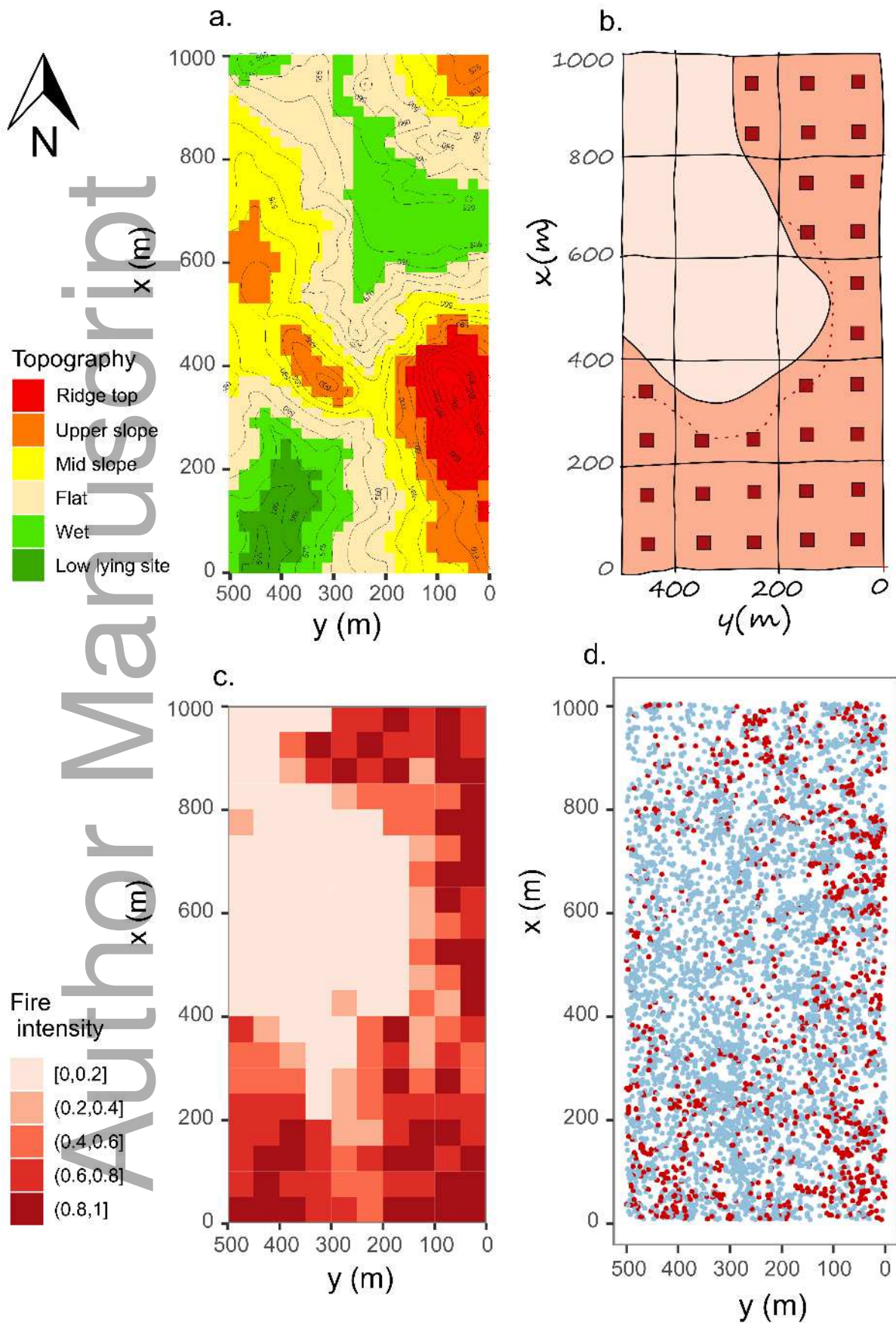
The species canopy status and forest type, tree growth, and mortality datasets used in this paper are available from the GitHub Repository: https://github.com/forestgeo/Trouve_et_al_2019

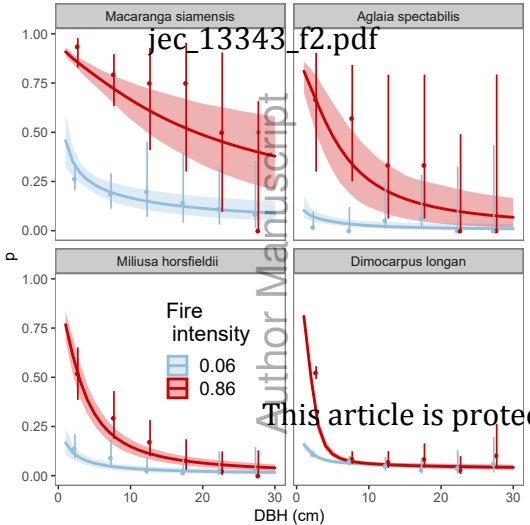
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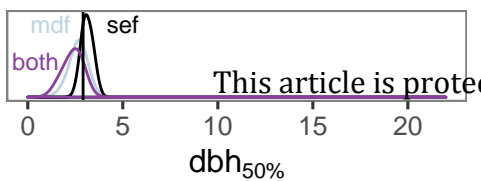
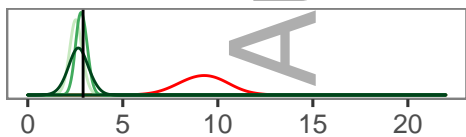
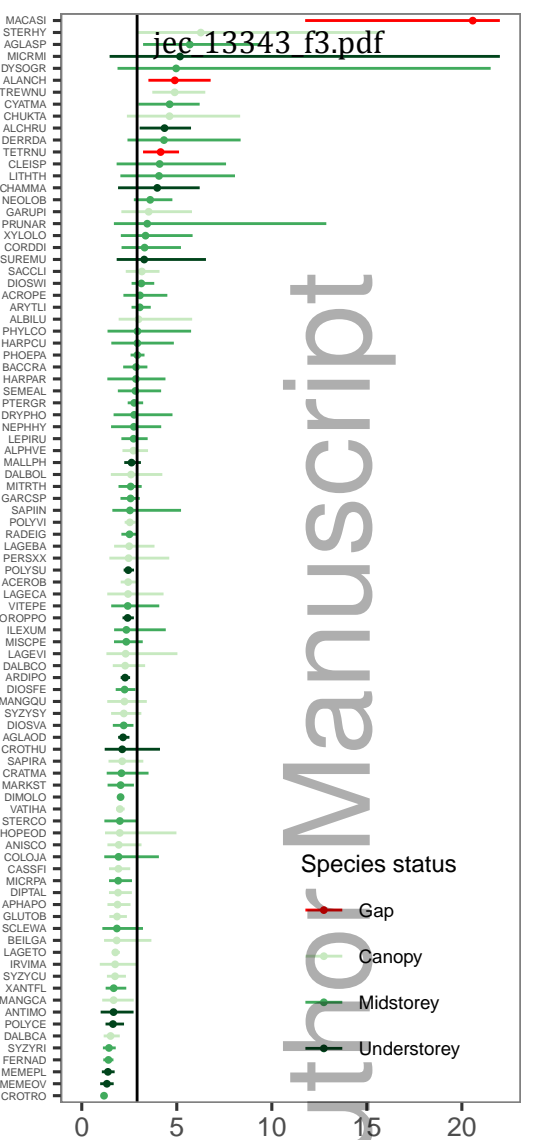
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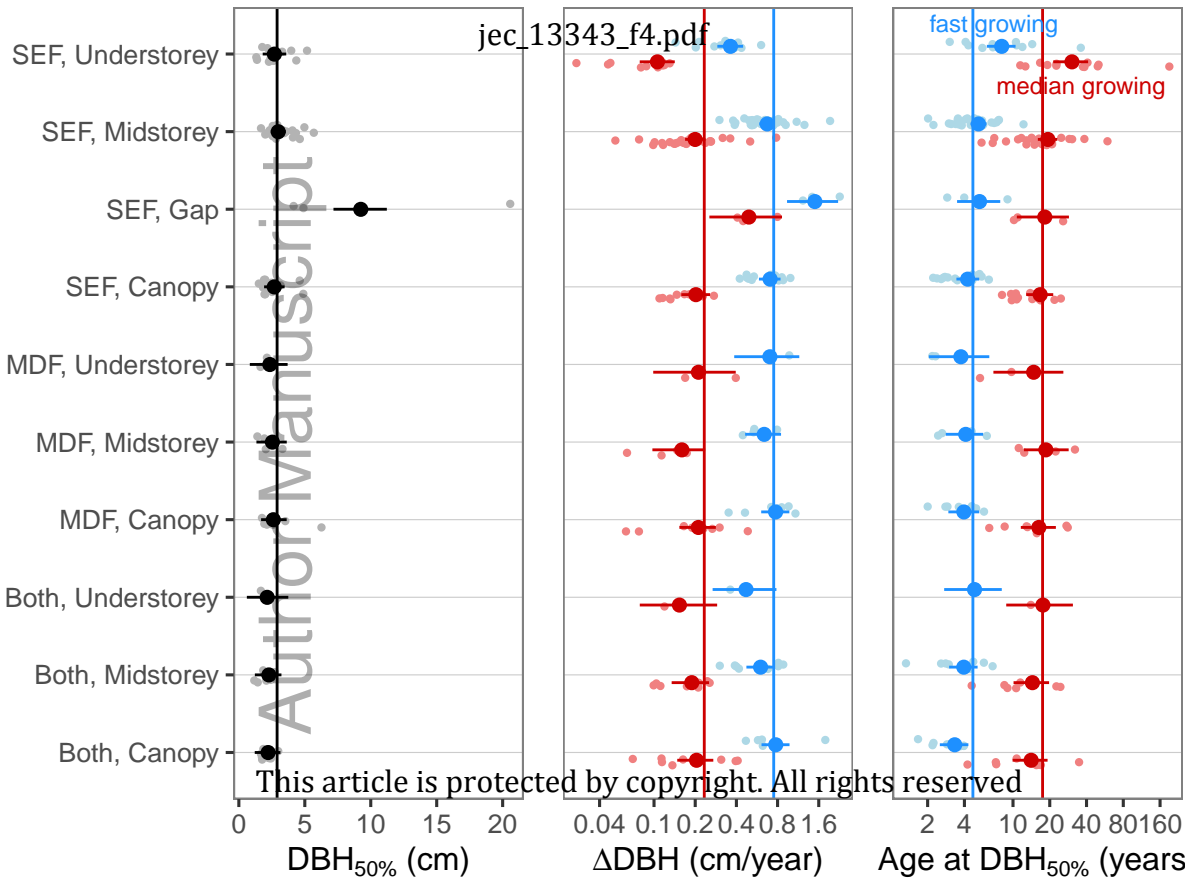




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