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The existence of a fire-mediated tree-recruitment bottleneck in an Asian savanna

Running title: Recruitment bottleneck in Asian savanna

Thuy T Nguyen[1*], Brett P. Murphy[2], Patrick J. Baker[1]

[1]School of Ecosystem and Forest Sciences, The University of Melbourne, Richmond 3121, Australia

[2]Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Northern Territory 0909, Australia

*Present address: Silviculture Research Institute, Vietnamese Academy of Forest Sciences, Ha Noi, Viet Nam.

Correspondence

Thuy T. Nguyen, Silviculture Research Institute, Vietnamese Academy of Forest Sciences, Ha Noi, Vietnam

Email: thuy.nguyen.um@gmail.com

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ABSTRACT AND KEYWORDS

Aim: A considerable proportion of the global savanna biome has been mis-classified as forest, especially in Asia. However, the structure and responses of dominant tree species to fire can help to clarify this ambiguity. Here, we examine demographic structure and fire responses of four dominant tree species in a deciduous dipterocarp forest (DDF) of the continental Southeast Asia. We examine whether fire creates a tree-recruitment bottleneck in the DDF, as in savannas on other continents.

Location: YokDon National Park, Vietnam.

Taxon: *Dipterocarpus tuberculatus* Roxb.; *Dipterocarpus obtusifolius* Teysm. ex Miq.; *Shorea obtusa* Wall. ex Blume; *Shorea siamensis* (Kurz) Miq.

Methods: We measured the size of all 8288 individuals of the four dominant dipterocarp species in 12 paired study plots. We then applied fire treatments (burnt or unburnt) to the plots and monitored the survival and growth of juveniles five times over the subsequent growing season.

Results: All four species showed clear indications of a recruitment bottleneck at the sapling stage. Almost all juveniles in the burnt plots suffered aboveground mortality, but 64% resprouted by the end of the following growing season. Compared to large juveniles, small juveniles had a significantly higher probability of aboveground mortality and a more limited ability to resprout. Within 3 months of fire, 43–93% of individuals had resprouted, and they had recovered 67–95% of their pre-fire basal diameter and 43–94% of their pre-fire height. At the end of the post-fire growing season, burnt juveniles experienced virtually no net increase in size; however, juveniles in unburnt plots attained up to 150% of their pre-fire size.

Main conclusions: The four dominant tree species of the DDF show remarkable similarities in the demographic structures and fire-responses with savanna tree species on other continents. Our results are consistent with the notion that the DDF is functionally similar to savannas on other continents. Fire appears to act as potent environmental filter of tree species composition in the DDF.

Keywords: Deciduous dipterocarp forest, fire, mesic savanna, resprouting, seedling growth, seedling mortality, tree demography, tropical dry forest, YokDon National Park.

1 INTRODUCTION

Fire is one of the key factors determining global vegetation patterns, especially in the tropics (Bond *et al.*, 2005; Staver *et al.*, 2011; Murphy & Bowman, 2012). When fire is suppressed, a large proportion of the Earth's open vegetation is predicted to transition to closed forests. The regions thought to be at highest risk of such biome switching are parts of South America and Asia (Hirota *et al.*, 2011; Lehmann *et al.*, 2011; Staver *et al.*, 2011). In these 'bistable' regions, savannas with high tree cover can exist in high-rainfall areas, and such formations have often been mistaken for 'true' forests, especially in Asia (Stott, 1990; Ratnam *et al.*, 2011; Ratnam *et al.*, 2016, Nguyen & Baker, 2016). Fire is critical to the maintenance of savannas in these areas and are strongly associated with many structural features, functional traits and regeneration strategies characteristic of savanna trees species (Ratnam *et al.*, 2011; Ratnam *et al.*, 2016).

Parts of tropical Asia with high rainfall seasonality experience frequent landscape-scale fires. These fires most often occur in natural vegetation characterised by an open, discontinuous tree layer and a continuous C_3 or C_4 grass layer (Stott, 1988). While such vegetation types have been tentatively identified as high-biomass mesic savannas, they have most often been regionally classified as degraded tropical forests or tropical dry forests (Stott, 1990; Ratnam *et al.*, 2011; Ratnam *et al.*, 2016). A notable example of ecosystems of this type is the deciduous dipterocarp forest (DDF) of continental Southeast Asia (Ratnam *et al.*, 2011). Whether the DDF, and other similar ecosystems in the region (i.e., characterized by a homogeneous tree layer over a continuous grass layer, and by frequent low-intensity fires), are savanna or forest is of critical importance if they are to be managed appropriately to sustain their economic, ecological, and cultural values (Ratnam *et al.*, 2011). These ecosystems are a key part of the Indochinese 'biodiversity hotspot', so classified because of the region's remarkable endemic biodiversity and the high rates of habitat degradation (Myers *et al.*, 2000). To clarify and provide science-based management practices for these ecosystems, it is important to understand their defining features and the roles of fire in shaping their structure and function. In this context, the DDF is an ideal model system to explore whether well-established concepts of savanna ecology, such as fire-mediated tree recruitment bottlenecks (Higgins *et al.*, 2000; Bond, 2008; Prior *et al.*, 2010), are applicable to the high-biomass mesic savannas of Asia.

A large proportion of savanna ecology literature focuses on the effects of fire on the structural and functional dynamics of savannas. This provides a strong conceptual background for understanding the role of fire in driving the tree dynamics of the DDF of continental Southeast

Asia. Although numerous studies have observed fire-mediated bottlenecks in the stand structure of savanna tree species (see Werner & Prior, 2013, and citations therein), there are few studies that focus on critical demographic transitions of savanna trees, especially of juvenile to sapling stages (Midgley *et al.*, 2010). Little is known about how juvenile savanna trees become saplings and adults given the occurrence of frequent fires that severely limit seedling and sapling growth. Bridging these knowledge gaps will advance our understanding of fire as a key factor driving the structure of savanna ecosystems. To do this requires detailed studies of post-fire recovery of individual trees in savanna communities.

In this study, we describe the demographic structure of the four dominant tree species of the DDF and use an *in situ* fire experiment to describe: (1) the effects of fire on aboveground and whole-plant mortality of juveniles in the DDF; and (2) patterns of juvenile resprouting and growth following fire. By studying the post-fire recovery of large numbers of juveniles, we shed light on how juveniles become saplings in a fire-prone Asian savanna. We use these findings to consider the role of fire as an environmental filter of tree species composition in the DDF.

2 MATERIALS AND METHODS

2.1 Study site

The study was conducted in YokDon National Park (YokDon NP) in the Central Highlands of Vietnam (Fig. 1; 12.702°N, 107.716°E). YokDon NP covers an area of 1155 km^2 and protects the largest remaining area of DDF in Vietnam. The park's topography is relatively flat, with an average elevation of 200 m above sea level and the highest point at 482 m (Ho, 2008). YokDon NP has a strong seasonal climate with mean annual rainfall of 1610 mm (87% occurring in the wet season, May–October) (Dinh, 1993). The dry season lasts for 4–6 months with three months of <10 mm rainfall (Dinh, 1993)..

DDF covers 80% of YokDon NP and the remaining vegetation within the National Park is either evergreen or semi-evergreen forest, or bamboo patches (Ho, 2008). The canopy layer of the DDF in YokDon NP is dominated by four deciduous dipterocarp tree species: *Dipterocarpus obtusifolius, D. tuberculatus, Shorea obtusa* and *S. siamensis* (Tran, 1991; Dinh, 1993; Nguyen & Baker, 2016). These four species form distinct assemblages where only one or two species account for the majority of tree basal area at the stand level (Tran, 1991; Dinh, 1993; Nguyen & Baker, 2016). A mid-storey is usually absent (Kutintara, 1975; Bunyavejchewin *et al.*, 2011; Nguyen & Baker, 2016), while the under-storey consists of a continuous layer of shade-intolerant C_3 and C_4 grasses, forbs and abundant juveniles (resprouts and true seedlings) of the dominant tree species (Nguyen & Baker, 2016).

In the dry season (November–April), canopy trees shed their leaves, grasses senesce, and woody juveniles dry out, resulting in a highly combustible surface fuel layer. DDF in YokDon NP has been managed under a regime of extensive prescribed burning since it was established in 1992 (Ngo, 2007). The annual prescribed burning regime typically results in a mosaic of burnt and unburnt patches across the YokDon NP landscape (T. Nguyen, pers. obs.). Based on MODIS satellite-derived burnt area data (Giglio *et al.*, 2016), between November 2000 and February 2018, an average of 72% of the Park burnt each year (Fig. 1).

2.2 Plot design

In late December 2014 and early January 2015, we selected 12 sites at which to conduct the fire experiment (Fig. 1). To ensure the presence of all four dominant dipterocarp tree species in the measurements, each site represented one species assemblage with each assemblage replicated three times.

We randomly divided each site into two plots, one to be burnt and one to remain unburnt (i.e., control). The burnt and unburnt plots were <20 m apart, with the exception of one site with plots ca. 40 m apart. The abiotic and biotic conditions (e.g., soil type, canopy cover, grass abundance) of the two plots at each site were relatively homogeneous. Each unburnt plot consisted of a single 10 × 10 m block, while each burnt plot consisted of three 10 × 10 m blocks, separated by 2-m wide firebreaks. The three-block fire treatment was originally intended to introduce three fuel load scenarios (low, medium, and high) based on manipulating grass biomass within each block. However, before conducting the burning, we observed that grasses contribute less to the amount of fuel load than dried leaves, particularly in the *D. tuberculatus*-dominated assemblages. Thus, we decided not to manipulate the grasses in any of the plots. The separation of the three blocks also allow us to better manage the fire and more accurately record the fire temperature during the experiment.

2.3 Pre-fire measurements

After the plots were established, all individual trees of the four dominant deciduous dipterocarp species within the burnt and unburnt plots, regardless of size (7710 juveniles and 578 adults), were tagged, measured, and identified to species. The locations of all 8288 individuals were mapped within each plot. Tagging and recording the position of each individual tree allow us to re-locate most of them in post-fire measurements (only one of

7710 juveniles was unable to be relocated). While tagging, mapping, and measuring the juveniles, we tried to minimise any impacts on the grass and seedling layer.

Juveniles were defined as individuals having a diameter at breast height (DBH; 130 cm above the ground) of <1 cm, and included true seedlings (i.e., recent germinants), resprouts, and root suckers. We distinguish recently germinated seedlings (true seedlings) from older juveniles. From our experience of measuring tens thousands of seedlings in the DDF, we could readily distinguish true seedlings (<6 months old) from older juveniles, including resprouts and root suckers. True seedlings of all four species could be easily distinguished from previous years' seedlings (even of the same size) by paler green leaves and (soft) stem. In addition, the remains of the seed are usually visible for an extended period of time for true seedlings of the *Dipterocarpus* species because the seeds are relatively large (~8 g for both species). However, this is not the case for the *Shorea* species because their seeds are much smaller (~0.8 g for *S. obtusa* and 2 g for *S. siamensis*) and they decompose soon after germination. After the first dry season, it is impossible to distinguish the origin and the age of juveniles.

For each juvenile, we counted the number of stems, recorded whether it was a recent seedling or older juvenile, measured the basal diameter of the largest diameter stem using digital calipers, and measured the height of the largest diameter stem using a long ruler. For individuals with DBH ≥1 cm (referred to as adults), we measured DBH using a diameter tape and height using a measuring pole or clinometer.

After measurements in the plots (i.e., at the end of January and early February 2015), we created a 5-m firebreak around each burnt and unburnt plot to prevent fire spreading in or out of the experimental plots. Burning of the plots occurred between 27 February and 9 March 2015, mostly between13.00 and 15.30. Prior to burning, eight thermocouple probes were installed in a grid across each burnt block at a height of 20 cm to record fire temperatures. As installing the thermocouple probes, we observed the aboveground mortality of small juveniles in burnt and unburnt plots.

2.4 After fire measurements

Immediately after the burning experiment, we assess the aboveground survival of all juveniles. We also verified the aboveground survival status again at the first post-fire measurement (i.e., at four weeks after fire). Juveniles that suffered aboveground mortality (in either burnt or unburnt plots) started resprouting about three weeks after the experimental burning occurred. We made the first post-fire assessment of juvenile survival and growth at the end of the fourth week after fire. For the first post-fire assessment, we checked all juveniles for the presence/absence of live shoots and measured basal diameter and height of the largest diameter live shoots. We refer to new shoots, produced following the death of the existing shoot, as 'resprouts'. For resprouts that were too small or short to measure diameter and height, we simply counted the number of stems present. Subsequent measurements on the burnt plots were conducted at 6, 8, and 10 weeks and the last measurement was conducted at the end of the wet season, 32 weeks after the experimental burning occurred. In the unburnt plots we undertook the same measurements at 4, 10, and 32 weeks only, because the growth of live juveniles appeared to be negligible during the first few weeks after the fires were set in the burnt plots. In both burnt and unburnt plots, juveniles that suffered aboveground mortality after fire, yet had not resprouted during the 32 weeks after the experimental fire were considered entirely dead (i.e., whole-plant mortality). A chronosequence of fixed-point photographs in one of the burnt plots are provided in Appendix 1.

Of the 12 sites, one *S. obtusa*- and one *D. tuberculatus*-dominated site were accidentally burnt by local villagers. One site was burnt at about the same time as the experimental fires, and one was burnt 4 weeks earlier. Because the earlier burn occurred at the peak of the dry season, the juveniles that suffered aboveground mortality in the accidentally burnt plots did not resprout noticeably earlier than those in the deliberately burnt plots. We decided to continue post-fire measurements on these two accidentally burnt sites as we did for the other ten sites. Since the plots assigned to the no-fire treatment were burnt at these two sites, we merged them with the burnt plots at the same site. As such we retained the full 12 sites, but two sites lacked the no-fire controls.

2.4 Data analysis

We first investigated the height distribution of all 8288 individuals of the four dipterocarp species. We focused on the height distribution because the diameters of juveniles and adults were measured at different locations on the stem (i.e., basal diameter vs. DBH). We used Hartigan's dip test in the 'diptest' package (Maechler, 2015) in R (R Core Team, 2017) to test unimodality of the height distribution.

To describe how juveniles resprout over time, we calculated the additive proportion of live shoots over six measurements for burnt plots and four measurements for unburnt plots. To understand how the resprouts grew over time in the burnt plots, we calculated the average growth in diameter, height, and the number of stems of early and late resprouting juveniles over six repeated measurements. We refer to early and late reprouters as those juveniles that resprouted at 3-4 weeks and 7-8 weeks following fire, respectively. The two pulses of resprouting (i.e., early and late resprouting) were pronounced in the field and revealed on the graph of additive proportion of live shoots. Similarly, in the unburnt plots, we calculated the average growth of juveniles that suffered aboveground mortality yet resprouted 3-4 weeks after the fire (i.e., early resprouters) and the growth of juveniles that did not suffer aboveground mortality (survivors). We also presented the juveniles' sizes before vs. after fire and the pre-fire size vs. the increment over 32 weeks following fire. For all four species, we calculated the 95th percentile of diameter and height increment over the 32 weeks following fire.

Factors affecting the aboveground mortality were explored using a generalized linear mixed effects model (GLMM), with binomial errors and a logit link function. Site was treated as a random intercept in all models. In the GLMM, the status of all individuals immediately after fire (i.e., aboveground mortality vs. survival) was treated as the response variable. The pre-fire height, species, and fire treatment (i.e., fire vs. no fire) were treated as the predictor variables. The pre-fire height was centred and standardised before being used in the model. We excluded 119 juveniles that died over the wet season from the 7710 juveniles because their mortality was not caused by the treatment. All of the 119 juveniles were <25 cm height and including 78 true seedlings out of 108 individuals with a single stem. In total, we used the data of 8169 juveniles and adults for modelling. All the analyses were performed in R (version 3.3.3; R Core Team, 2017) with the function 'glmer' from the package 'lme4' (Bates et al., 2015).

3 RESULTS

3.1 Demographic structure

Juveniles (<1 cm DBH) accounted for 93% of the 8288 individuals measured at the 12 sites. True seedlings (all ≤25 cm tall) accounted for 33% of juveniles, while resprouts and root suckers ≤25 cm tall accounted for 42%. For juveniles only, we referred to all individuals ≤25 cm tall (including true seedlings, resprouts, and root suckers) as *small* juveniles and individuals >25 cm tall as *large* juveniles. The demographic structure of the four dominant tree species prior to the burning experiment was not unimodal (p = 0.004 for *S. siamensis* and p <0.0001 for the three other species). The demographic structure of the three species other than *S. siamensis* showed a pronounced lack of individuals 100–400 cm tall (Fig. 2). *Shorea* *obtusa* had the fewest individuals within this range, followed by *D. obtusifolius*. Perhaps most notably, small juveniles of *S. siamensis* were extremely scarce (Fig. 2).

3.2 Aboveground mortality, whole-plant mortality, and resprouting of juveniles

Almost all (99.6% of 6465) juveniles in the burnt plots suffered aboveground mortality regardless of their pre-fire size (0.3-37 mm basal diameter and 2–173 cm tall) and the maximum fire temperature (mean of maximum temperature from all thermocouples in each burnt plot ranged from 307–666^{o}C). In marked contrast, in the unburnt plots, only 31% of 1245 juveniles suffered aboveground mortality in the absence of fire over the same period of time (Fig. 3).

True seedlings were much more likely to suffer aboveground mortality than resprouts. Despite true seedlings representing 36% of juveniles in the burnt plots and 21% of juveniles in the unburnt plots, they constituted 71% and 53% of aboveground mortality of juveniles, respectively.

In both burnt and unburnt plots, resprouting by individuals that suffered aboveground mortality commenced approximately three weeks after the fire. In both the burnt and unburnt plots most resprouting occurred within ~10 weeks of the fire (Fig. 3). The patterns of resprouting, represented as the additive proportion of all juveniles with live shoots (Fig. 3), were very similar between *D. tuberculatus* and *S. siamensis* and, to a lesser extent, between *D. obtusifolius* and *S. obtusa*. *Dipterocarpus tuberculatus* and *S. siamensis* resprouted earlier and had far greater stem survival rates than *D. obtusifolius* and *S. obtusa* (Fig. 3). However, in both burnt and unburnt plots, the resprouting pattern of D*. tuberculatus* and *S. siamensis* were reversed between small and large juveniles (Fig. 3). The high mortality of small juveniles of *S. siamensis* may explain their poor abundance in the demographic structure (Fig. 2).

At the end of the study (i.e., 32 weeks after fire), the overall whole-plant mortality rate for juveniles in the burnt plots (36%) was almost 2.5 times greater than in the unburnt plots (14.6%). In the burnt plots, the highest mortality rate was among juveniles of *S. obtusa* (56%), followed by *D. obtusifolius* (33%); the mortality rate of juveniles of *D. tuberculatus* and *S. siamensis* was only 7% each (Fig. 3). In the unburnt plots, juveniles of *D. obtusifolius* had the highest mortality rate (21%), followed by *S. obtusa* (16%), *S. siamensis* (15%), and *D. tuberculatus* (9%) (Fig. 3). This pattern is consistent with the number of true seedlings of *S. obtusa*, *D. obtusifolius*, *D. tuberculatus* and *S. siamensis* in the burnt (2054, 194, 44, and 19, respectively) and unburnt plots (115, 115, 28 and 7, respectively).

The GLMM suggested that the probability of aboveground mortality was related to pre-fire height, fire treatment (i.e, burnt or unburnt), and species (Table 1), with pre-fire height having the largest positive effect, followed by the fire treatment. The probability of stem survival increasing with increasing pre-fire height (Fig. 4) and was significantly greater in the unburnt plots (Table 1). Individuals <100 cm tall had <10% chance of stem survival following fire (i.e., >90% chance of aboveground mortality), while above this height the probability of stem survival sharply increased (Fig. 4). Above 300 cm tall, the probability of stem survival was very high (>90%) (Fig. 4). In general, the probability of stem survival was not significantly different for *S. obtusa*, *S. siamensis* and *D. obtusifolius* and was far greater for *D. tuberculatus* (Table 1, Fig. 4).

3.3 Juvenile growth over the wet season

In burnt plots, the growth patterns of the four deciduous dipterocarp species (both early and late resprouters) were similar (Fig. 5). Top-killed juveniles obtained the majority of their pre-fire size within 10 weeks following fire (i.e., before the peak of the wet season). Subsequent growth over the 22 weeks of the wet season was relatively limited (Fig. 5). Early resprouters in the burnt plots grew markedly within 3-4 weeks of fire, regaining up to 63% of their pre-fire basal diameter and 58% of pre-fire height (Fig. 5). Similarly, late resprouters in the burnt plots re-gained up to 75% of their pre-fire basal diameter and 74% of their pre-fire height in just two weeks of resprouting (Fig. 5). The number of stems of early resprouters in the burnt plots also gradually increased, peaked at about 6-10 weeks after fire and decreased slightly over the wet season (Fig. 5). Noticeably, juveniles that resprouted 3-4 weeks after fire had much larger pre-fire sizes and the number of stems than those resprouted 7-8 weeks after fire (y-axis on Fig. 5).

In unburnt plots, early resprouters also obtained up to 70% of their initial basal diameter and up to 81% of their initial height at 4 weeks after experimental burning occurred (Fig. 5). However, regardless of being burnt or not, juveniles that suffered aboveground mortality failed to gain a significantly increase in size by 32 weeks following fire. An exception was early resprouting *D. tuberculatus* individuals in the unburnt plots; this group attained 142% of the pre-fire height (Fig. 5). In marked contrast, unburnt juveniles gained up to 139% of their pre-fire basal diameter and 150% of their pre-fire height in one growing season (Fig. 5).

The effects of fire/no fire on juvenile growth by 32 weeks following fire were even clear when all juveniles regardless of their status (presented in Fig. 5) were pooled (Fig. 6). With fire presence, size distribution, particularly, basal diameter distribution of all juveniles by 32 weeks following fire appeared almost no distinct difference from those before fire (Fig. 6). However, without fire, both basal diameter and height distribution of juveniles at 32 weeks following fire distinctively departed from the pre-fire size distributions (Fig. 6).

3.4 Growth strategies in response to fire

The four species appeared to have different growth strategies over the course of the growing season following fire, depending on whether they were suffered aboveground mortality or not. All juveniles that suffered aboveground mortality had a far greater growth rate in the first 10 weeks following fire (i.e., prior to the wet season) than the subsequent 22 weeks (i.e., during the wet season) (Fig. 5). As a result, all such juveniles, regardless of whether they resprouted early or late, re-gained most of their pre-fire size by 10 weeks following fire, but grew little in the subsequent 22 weeks (Fig. 5).

However, the growth of juveniles that did not suffer aboveground mortality in the unburnt plots revealed different patterns. These individuals did not appear to grow (and in some cases had a net reduction in size) in the first 4 weeks after experimental burning occurred (Fig. 5). It was only with the onset of the wet season that these individuals increased in both basal diameter and height. Notably, most species in the unburnt plots grew more (proportionally) in height than basal diameter in the first 10 weeks following fire in the burnt plots, while growing more in basal diameter than height in the subsequent 22 weeks (Fig. 5). Juveniles that suffered aboveground mortality in the burnt plots tended to produce more shoots than juveniles in the unburnt plots (Fig. 5).

Large juveniles, particularly in burnt plots, often failed to regain their pre-fire sizes (Fig. 7). In contrast, some mid-size juveniles appeared to have exceptional growth in both burnt and unburnt plots. Strikingly, some *S. siamensis* individuals gained up to approximately 15 mm in basal diameter and 50 cm height regardless of being burnt or not. In the burnt plots, the 95th percentile of both diameter and height increment (i.e., the 5% of fastest-growing individuals) of *S. siamensis* was at least double those of the other species (data not shown). However, without fire, the 95th percentile values of basal diameter and height increment for *S. siamensis*, *D. tuberculatus* and *D. obtusifolius* were similar (approximately 50 cm in height and 7–8 mm in basal diameter over one year). Mean height growth in the absence of fire for the 95th percentile juveniles was 32–53 cm year^{-1}.

4 DISCUSSION

Tropical savannas are characterised by strong recruitment bottlenecks – typically at the sapling stage – driven by top-down factors such as fire and herbivory (Higgins *et al.*, 2000;

Bond, 2008; Prior *et al.*, 2010; Lehmann *et al.*, 2014). Recruitment bottlenecks have been widely observed in the demographic structure and function of African (Higgins *et al.*, 2000; Wakeling *et al.*, 2011), Australian (Prior *et al.*, 2010; Werner & Prior, 2013), and South American savannas (Gardner, 2006; Hoffmann *et al.*, 2012). However, the relative paucity of studies describing demographic processes of savanna tree species have limited our understanding of their population dynamics (Midgley *et al.*, 2010). Most importantly, studies that quantify the strength of the recruitment bottlenecks and potential mechanisms, such as fire, are rare. Our burning experiment demonstrates the existence of a fire-mediated tree-recruitment bottleneck in the DDF of Southeast Asia – highlighting the congruence in the ecology of this ecosystem with the relatively well-studied savannas of Africa, Australia, and South America bottleneck (Higgins *et al.*, 2000; Gardner, 2006; Prior *et al.*, 2010; Wakeling *et al.*, 2011; Werner & Prior, 2013). Importantly, our results have demonstrated that the recruitment bottleneck in the DDF is driven by the effects of fire on juvenile mortality and growth – the bottleneck appears to occur at the transition from the juveniles to sapling (>1 m height) stages. Juveniles that were topkilled in burnt plots had virtually no net growth, whereas juveniles that did not suffer the aboveground mortality gained up to 139% in basal diameter and 150% in height, relative to their pre-fire size in one growing season (summer wet season).

The high rate of aboveground mortality of juveniles of the four deciduous dipterocarp species is similar to tree species in other mesic savannas. For example, Hoffmann and Solbrig (2003) reported that fire topkilled all individuals of shrub and small tree species in a Brazilian Cerrado (savanna). In another experiment, Hoffmann *et al.* (2009) demonstrated that fire topkilled 67% of trees of 4–5 cm diameter at 30 cm height. The high rate of aboveground mortality of individuals <2 m height in our study suggests that they are caught in the so-called 'fire trap' (Bond & Keeley, 2005). Below 2 m height, most individual trees have <40% chance of stem survival (Fig. 3) and they are often subjected to repeated cycles of fire, topkill, and resprouting at or below ground level. The exception was *D. tuberculatus*, which at a height of 2 m had >75% chance of not being topkilled by fire (Fig. 4).

Not only does pre-fire size dictate the ability of an individual to avoid aboveground mortality, but it is also strongly related to its ability to resprout if suffering from aboveground mortality. Among the life-history stages, small juveniles (including true seedlings) are the most vulnerable to fire because they are almost certain to be topkilled and then often fail to resprout. The high whole-plant mortality rates we observed for *S. obtusa* (56%) and *D. obtusifolius* (33%) juveniles was partly due to the high abundance of true seedlings that do not usually have enough carbohydrate reserve for resprouting (Gignoux et al., 2009). In an African savanna, the probability of seedling (<1 year old) mortality ranged from 0.37 to 0.9 and increased sharply for resprouts (>1 year old) (Gignoux et al., 2009). It was estimated that savanna species require 2-4 fires to reach a survival probability >0.9 (Gignoux et al., 2009). The Dipterocarp species in the present study are unlikely to reach the same survival probability at the same age.

In addition to fire, small juveniles of the DDF appear to be vulnerable to other factors including drought stress. In the unburnt plots, 31% of juveniles (mostly <25 cm height) suffered aboveground mortality at the end of the dry season. Most of this aboveground mortality may cause by drought stress as we observed from our repeated measurements on every single juvenile. Similarly, drought stress may be the main cause of aboveground mortality of many juveniles (particularly, true seedlings) in the burnt plots as we observed before fire was introduced. Marod *et al.* (2002) reported that drought alone caused whole-plant mortality of 68% of true seedlings and 46% of other small juveniles aged ≥1 year of *S. siamensis* in western Thailand. The vulnerability of juvenile savanna trees to both fire and drought suggests that climate-driven changes in the intensity of drought and fire weather in Southeast Asia are likely to alter tree recruitment rates, potentially with long-term impacts on structure and species composition of the DDF and other Southeast Asian savannas. Ratnam *et al.* (2016) have suggested that predicted intensification of rainfall in parts of South and East Asia may lead to the conversion of some areas of savanna to forest, but that it is difficult to predict the interacting effects of altered temperature, drought, and fire regimes on tree populations.

The underlying mechanisms that determine the timing of resprouting and growth rates of juvenile savanna trees are not well understood. Our post-fire measurements, taken a number of times over a full growing season, reveal that small juveniles not only experienced a higher aboveground mortality rate, but also resprouted much later than large juveniles (Fig. 5). The early resprouting of large juveniles allowed them sufficient time to recover their pre-fire sizes, while small juveniles did not require as much time. The rapid growth rate of juveniles immediately after resprouting has also been observed in other savannas (Schutz *et al.*, 2009), as well as seasonally tropical dry forest in India (Mondal & Sukumar, 2015). Schutz *et al.* (2009) suggested that in the first few months after fire, juveniles mobilise carbon from belowground organs for resprouting and grow rapidly to avoid later suppression by grasses. After this rapid growth period in which they re-build their aboveground parts, juveniles may switch from spending to storing carbon in the belowground organs (Schutz *et al.*, 2009). In contrast, juveniles that are not topkilled do not need to re-build their aboveground parts, instead resuming growth with the onset of the wet season (Fig. 5). The production of more stems by juveniles in the burnt compared to the unburnt plots (Fig. 5) may be a strategy for faster carbon replenishment.

The experiment demonstrated the benefits of avoiding aboveground mortality – whether due to fire, drought or other stressors. First, juveniles do not need to use their belowground carbon reserves to rebuild their aboveground parts. Second, juveniles have continuous development of bark thickness, diameter and height, which makes them even less susceptible to aboveground mortality in future dry seasons. Lawes *et al.* (2011) suggested that bark thickness is the most important factor determining the probability of fire survival because bark protects primary and secondary meristems from the damaging heat of fires. For Dipterocarp species, however, we observed that bark thickness, particularly, outer bark tends to be a genera-associated trait. At a certain height, outer bark thickness of the two *Shorea* species are usually far thinner than those of the two *Dipterocarpus* species.

Our study has demonstrated that large juveniles of the DDF often fail to gain sizes over a growing season (Fig. 7), much like juvenile trees in savannas on other continents (Hoffmann & Solbrig, 2003; Werner & Prior, 2013). Our results support the concept that only the fastest-growing juveniles can reach a threshold escape size (i.e., fire-resistant size) between successive fires (Wakeling *et al.*, 2011; Bond *et al.*, 2012). Mean height growth of the 95th percentile juveniles in the absence of fire in our study (32-53 cm year^{-1}) overlapped with analogous figures from an Australian mesic (~1500 mm annual rainfall) savanna 36-85 cm year^{-1}, calculated from the dominant tree species in Werner & Prior, 2013), but were somewhat lower than those from a South African mesic (~990 mm annual rainfall) savanna (53–90 cm year^{-1} in the absence of fire, Wakeling *et al.*, 2011). Given the height increments of the fastest-growing juveniles (Fig. 7) and the sizes required to avoid topkill by fire (i.e., >50% probability of survival: 1.8–2.5 m; Fig. 4), our results suggest that juveniles of the deciduous dipterocarp species require a number of consecutive fire-free years to reach a fire-resistant size and escape the fire trap (e.g., Zimmer & Baker, 2009). A key knowledge gap in the DDF, and other savannas globally, is the effects of repeated fires on the survival and growth of individual trees. While fire experiments such as ours, focusing on the effects of a single fire, provide important insights, there is a need for longer-term experiments (e.g. Higgins et al. 2007 in southern Africa, Russell-Smith et al. 2003 in Australia), with repeated fires, to understand how fire regimes affect stand structure.

Our results raise the question of whether fire filters tree species composition in the deciduous dipterocarp forest. We found that *D. tuberculatus* and *S. siamensis* experienced no increase in mortality following fire (Fig. 3) and had higher post-fire growth rates than *D. obtusifolius* and *S. obtusa* (Fig. 7). Thus, it is expected that they may have an advantage under a fire regime of very frequent (near annual), low-intensity surface fires – typical of contemporary fire regimes in YokDon NP. However, despite low mortality and high growth rates, *S. siamensis* also had the greatest height required to escape fire (Fig. 4). This may reflect that, among our four study species, *S. siamensis* had the thinnest outer bark at all sizes below 3 m height (T. Nguyen, unpublished data). The rapid growth of *S. siamensis* may compensate for its high probability of aboveground mortality, for a given stem size, and aid its transition through life stages in fire-free years. Small juveniles of *S. obtusa* appeared to be the most vulnerable to fire because of their high mortality and slow growth rate. The results suggest that juveniles of *D. obtusifolius*, *S. obtusa*, and *S. siamensis* require a relatively long fire-free period to reach their fire escape size, while juveniles of *D. tuberculatus* can become saplings even under an annual fire regime. This finding is consistent with observations of the dominance of *D. tuberculatus* in the majority of DDF sites at YokDon NP (Ogawa, 1965; Nguyen & Baker, 2016).

5 CONCLUSIONS

The four dominant tree species in the deciduous dipterocarp forest of YokDon NP exhibit demographic patterns consistent with a fire-mediated recruitment bottleneck, a well known phenomenon in the savannas of Africa, Australia and South America. Fire negatively impacts juvenile trees in the DDF in multiple ways. All juveniles are at high risk of suffering aboveground mortality, small juveniles are vulnerable to whole-plant mortality, and large juveniles are unlikely to recover their pre-fire size. However, resprouting following fire is often rapid and vigorous. As such, frequent fire maintains an abundant bank of juveniles, but a critical lack of saplings in the stand structure of the DDF. This is consistent with the proposed mechanism by which fire maintains an open tree canopy in mesic savannas throughout the tropics (Lehmann *et al.*, 2011; Hoffmann *et al.*, 2012; Murphy & Bowman, 2012). Chance periods of less frequent fire and higher rainfall are likely to trigger landscape-scale pulses of sapling recruitment. The four dominant canopy species of the DDF differed markedly in terms of stem survival, mortality rate, and growth responses after fire, and these differences are reflected in their patterns of abundance and dominance in the DDF in YokDon NP. Species that can escape the fire trap (e.g., *D. tuberculatus*) tend to dominate, making fire an important landscape-scale filter on tree species composition.

TABLE 1 Parameter estimates of the model of probability of stem survival, based on 8169 individuals in the analysis.

Model term	Estimate	Standard error	*p*
Intercept	-4.63	0.34	<0.0001
Pre-fire height	8.44	0.45	<0.0001
D. tuberculatus	1.32	0.28	<0.0001
S. obtusa	0.04	0.26	0.882
S. siamensis	-0.57	0.36	0.116
Unburnt	6.61	0.26	<0.0001

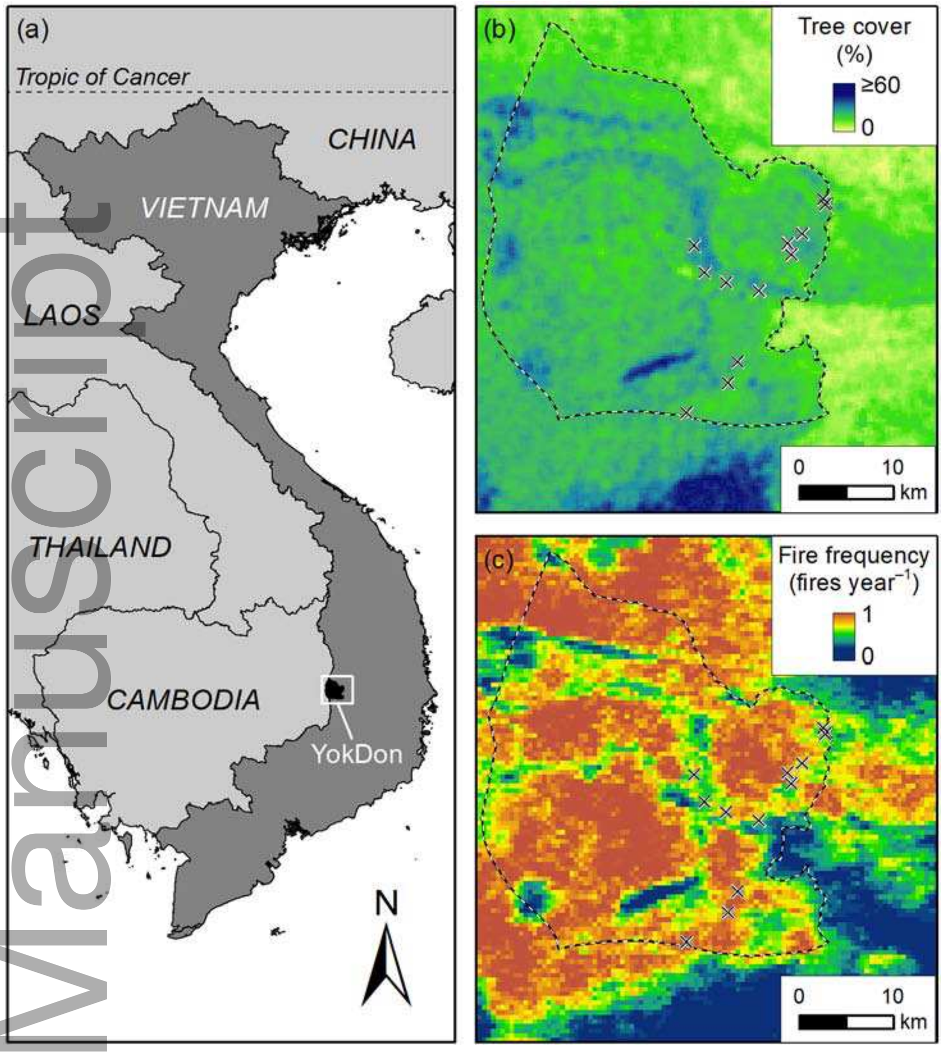

FIG. 1 (a) Location of YokDon NP within Vietnam. The boundary of YokDon NP is indicated by the black line in (b) and (c), with the crosses indicating the 12 sites where the fire experiment was conducted. In (b), tree cover (%) in 2015 is shown, based on MODIS satellite imagery (DiMiceli *et al.*, 2011). In (c), annualised fire frequency (fires year^{-1}), for the period November 2000 to February 2018, is shown, also based on MODIS satellite imagery (Giglio *et al.*, 2016).

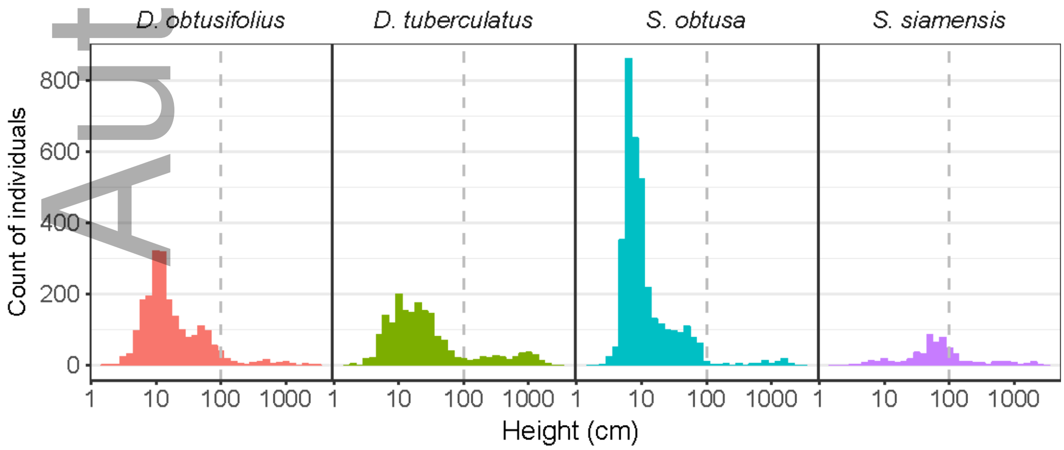

FIG. 2 Pre-fire height distribution of all 8288 individuals measured at the 12 study sites (*D. obtusifolius*, n = 2196; *D. tuberculatus*, n = 1914; *S. obtusa*, n = 3579; *S. siamensis*, n = 599). The x-axis is on a $\log_{10}$ scale. The vertical dashed line indicates a height of 100 cm, the approximate transition between juvenile and sapling stages.

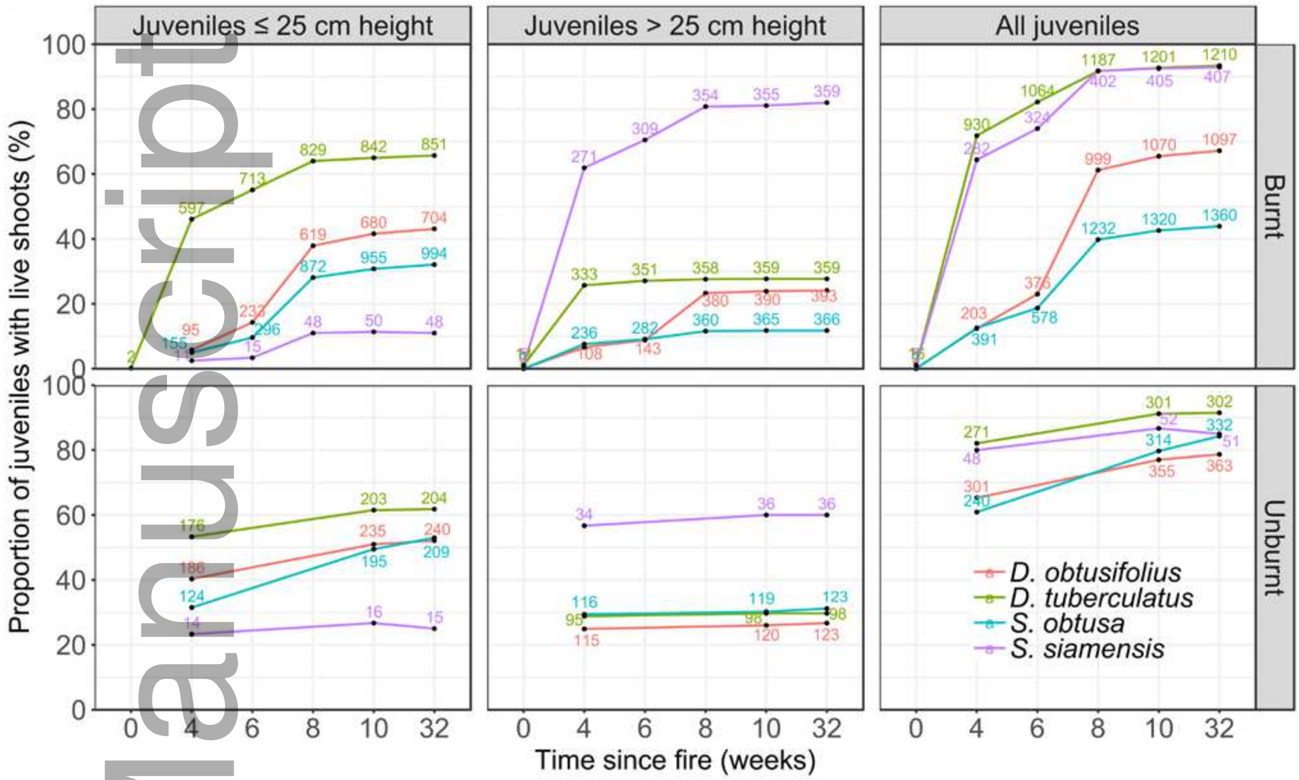

FIG. 3 The proportion of juveniles with live shoots in relation to time since fire in the burnt and unburnt plots. The small numbers next to each point represent the quantity of juveniles with live shoots at each measurement.

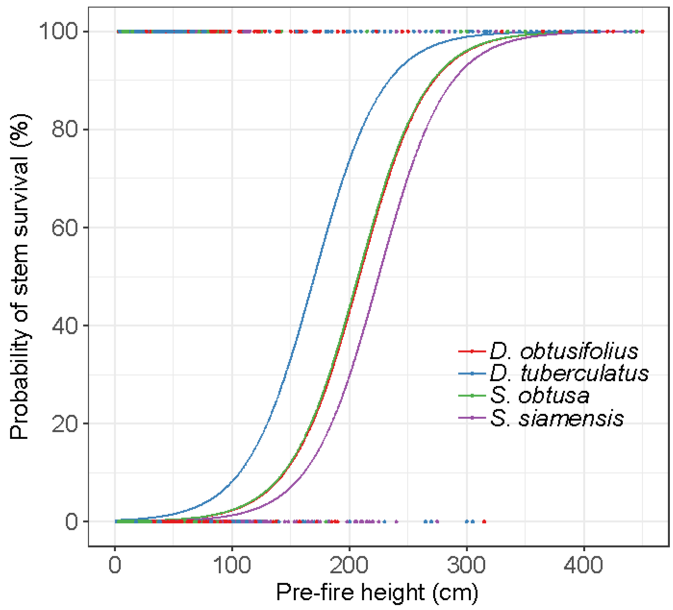

FIG. 4 Probability of stem survival in the burnt plots in relation to the pre-fire height, based on the predictions of a generalized linear mixed model.

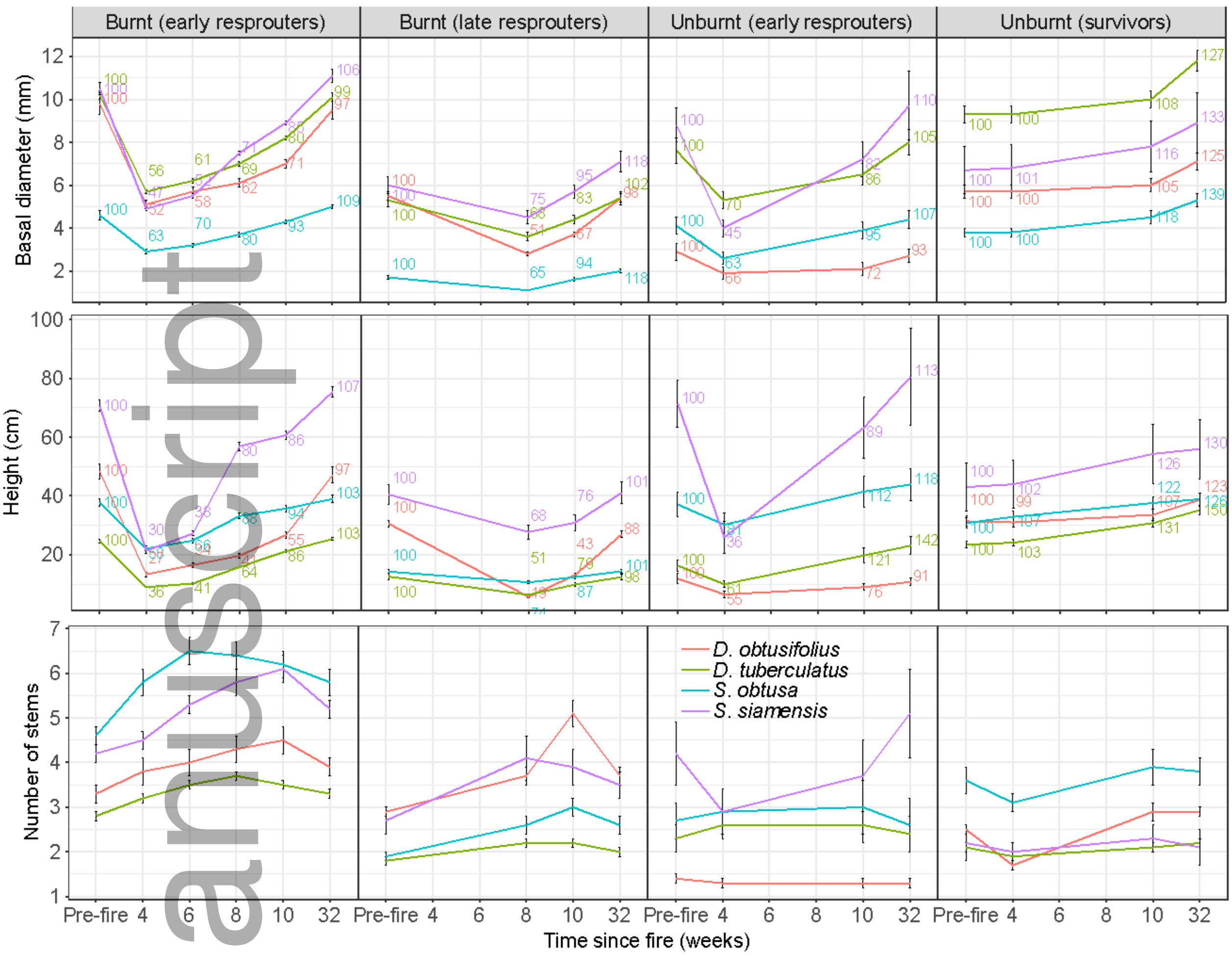

FIG. 5 Growth over time of basal diameter, height, and number of stems of juveniles that suffered aboveground mortality and resprouted early (3–4 weeks after fire) and late (7–8 weeks after fire); and juveniles that were not suffered aboveground mortality in the unburnt plots. The errors bars represent standard errors of the means. The small numbers next to the error bars indicate the ratio (%) of current size (basal diameter or height) to pre-fire size.

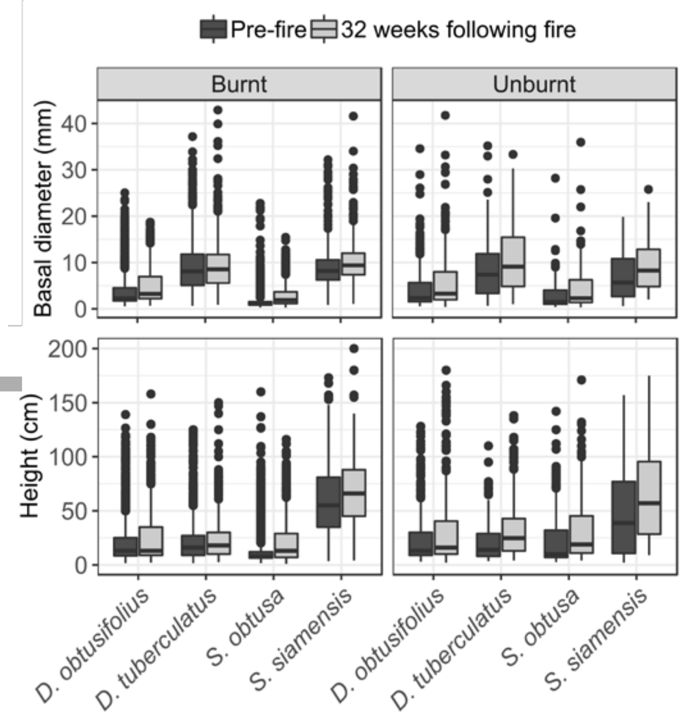

FIG. 6 Distribution of basal diameter (top panel) and height (bottom panel) of all juveniles before fire and at 32 weeks following fire.

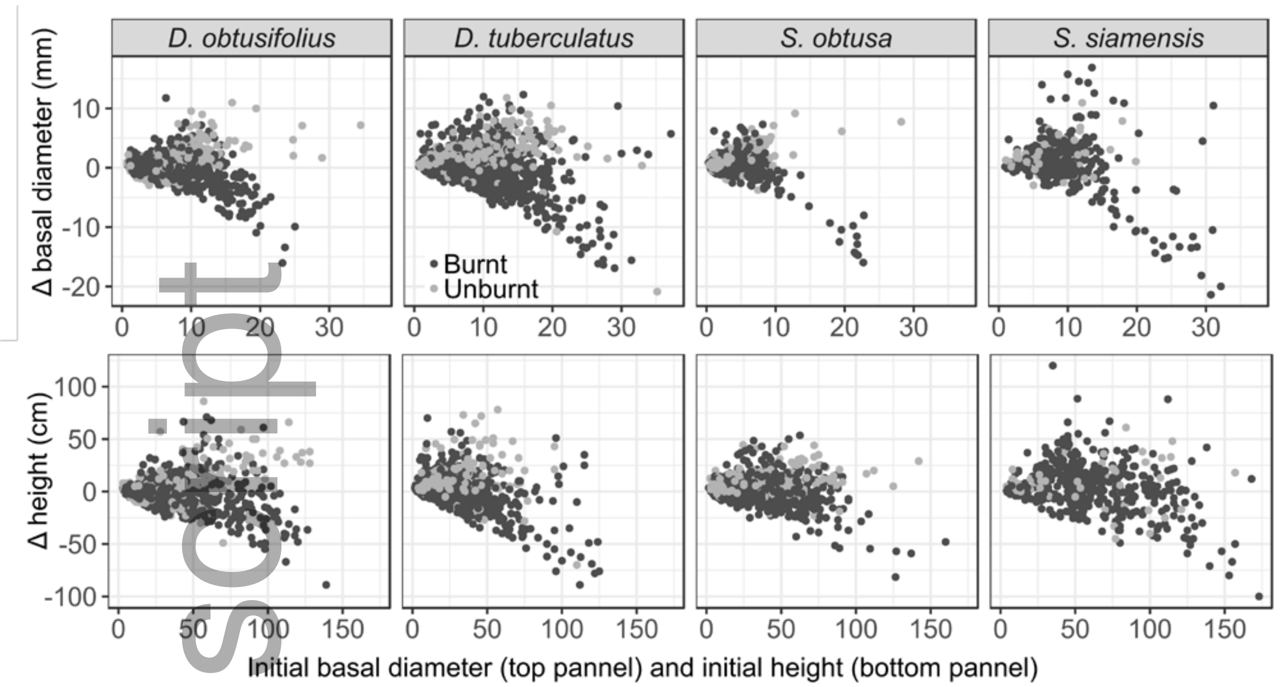

FIG. 7 Change in basal diameter (top panel) and height (bottom panel) of all juveniles in burnt and unburnt plots over 32 weeks compared to the pre-fire sizes.

APPENDIX 1: One burning plot (plot 10) dominated *D. tuberculatus* before creating the fire break strip (a), after burning (b). Juvenile of *D. tuberculatus* (c) and *S. obtusa* (d) resprouted at 4 weeks after fire in plot 10. Plot 10 at 7-8 weeks following fire (e) and 9-10 weeks after fire (f).

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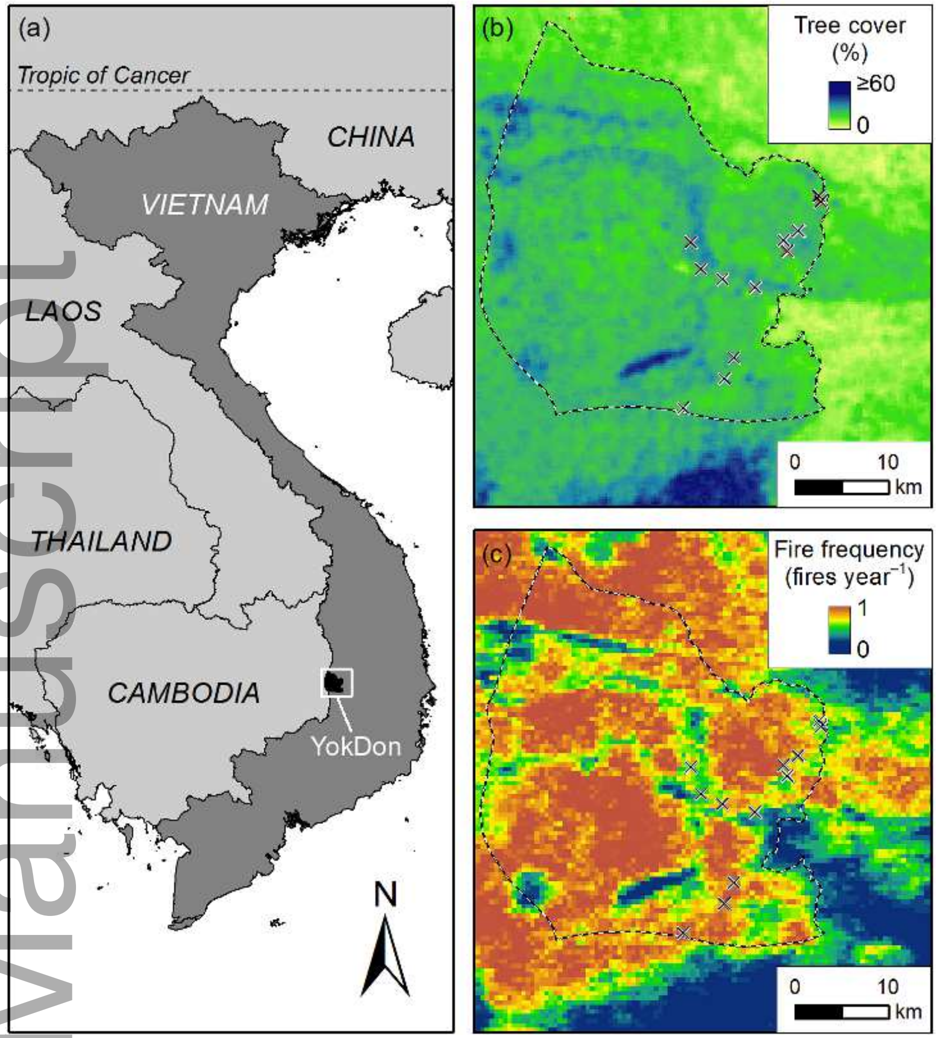
BIOSKETCHES

Thuy T. Nguyen's research focuses on ecological factors that drive community structure, biodiversity and dynamics of tropical vegetation types e.g., savannas and forests.

Brett P. Murphy's research focuses on understanding how fire has shaped and maintains the biota of tropical savanna landscapes, and how contemporary fire regimes can best be managed for biodiversity conservation in northern Australia, especially in relation to declining small mammals and fire-sensitive vegetation communities.

Patrick J. Baker's studies how trees and forests change over time and how this understanding can be used to develop better forest management systems. He maintains active research programs in palaeoclimatology, forest stand dynamics, and silviculture.

Author contributions: TTN, PJB and BPM conceived the ideas. TTN collected the data. TTN performed the analyses with contributions from BPM and PJB. TTN led the writing with substantial contributions of BPM and PJB.



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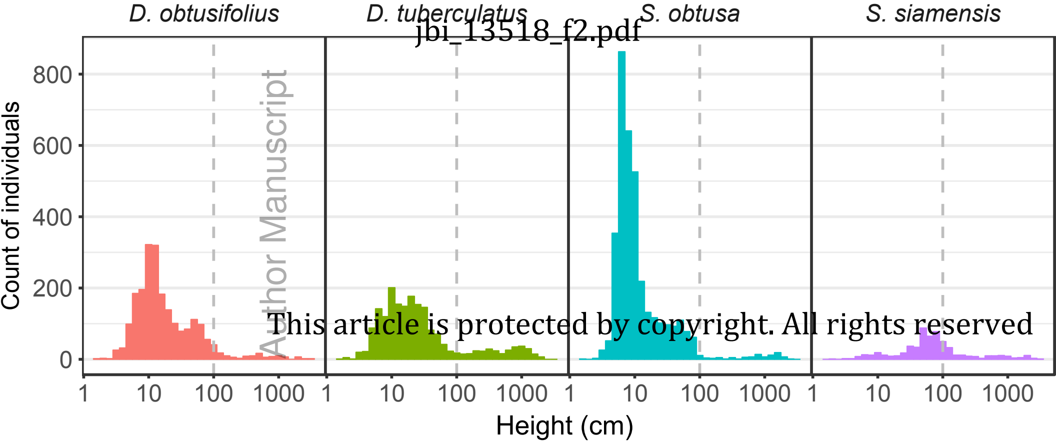
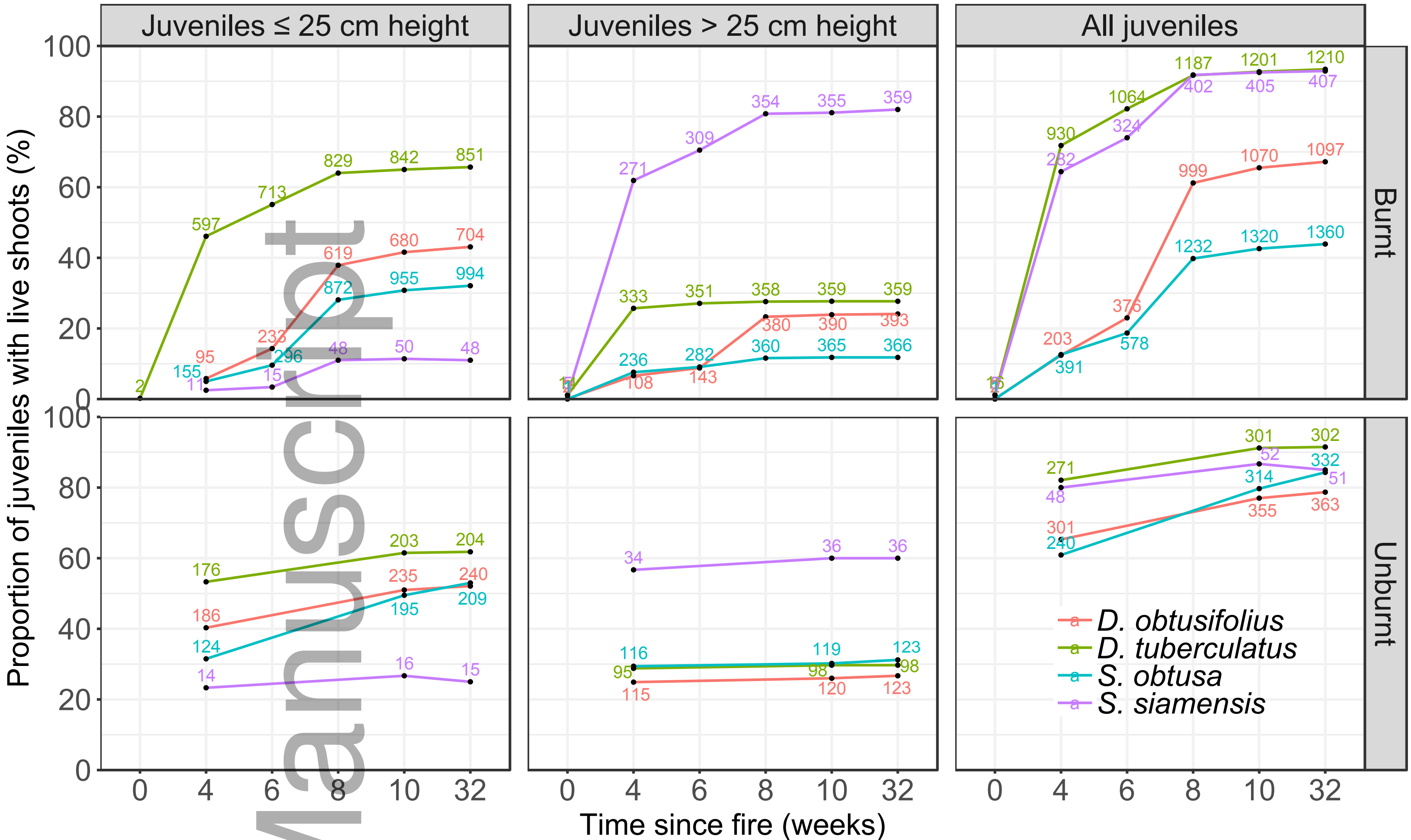

D. obtusifolius
D. tuberculatus
S. obtusa
S. siamensis
Count of individuals
800
600
400
200
0
1
10
100
1000
Height (cm)



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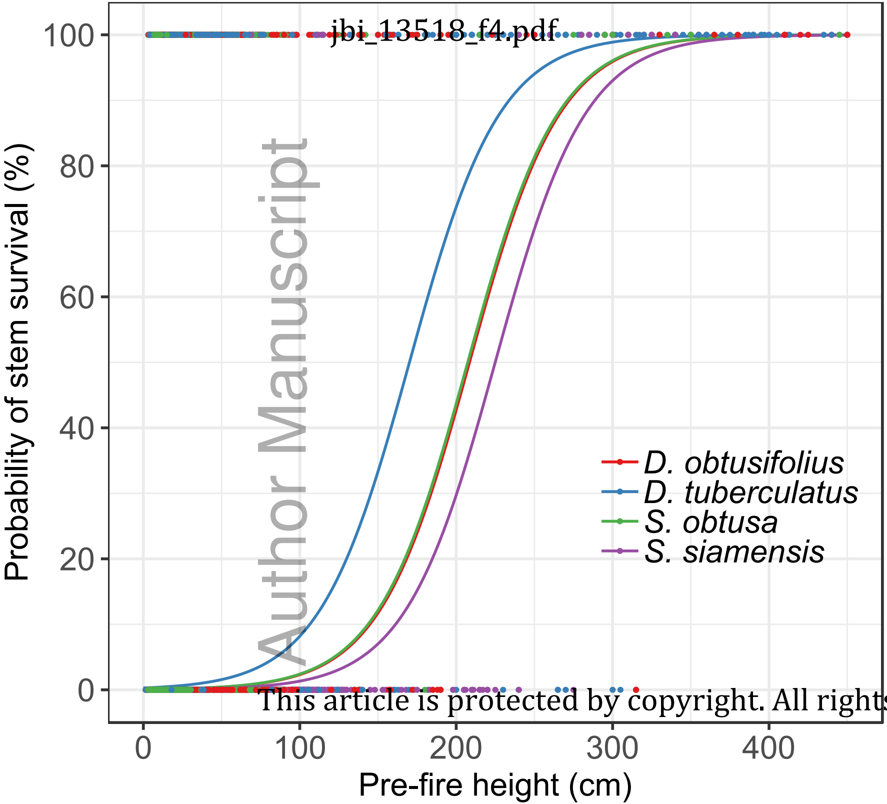
Probability of stem survival (%)
100
80
60
40
20
0
Pre-fire height (cm)
0
100
200
300
400
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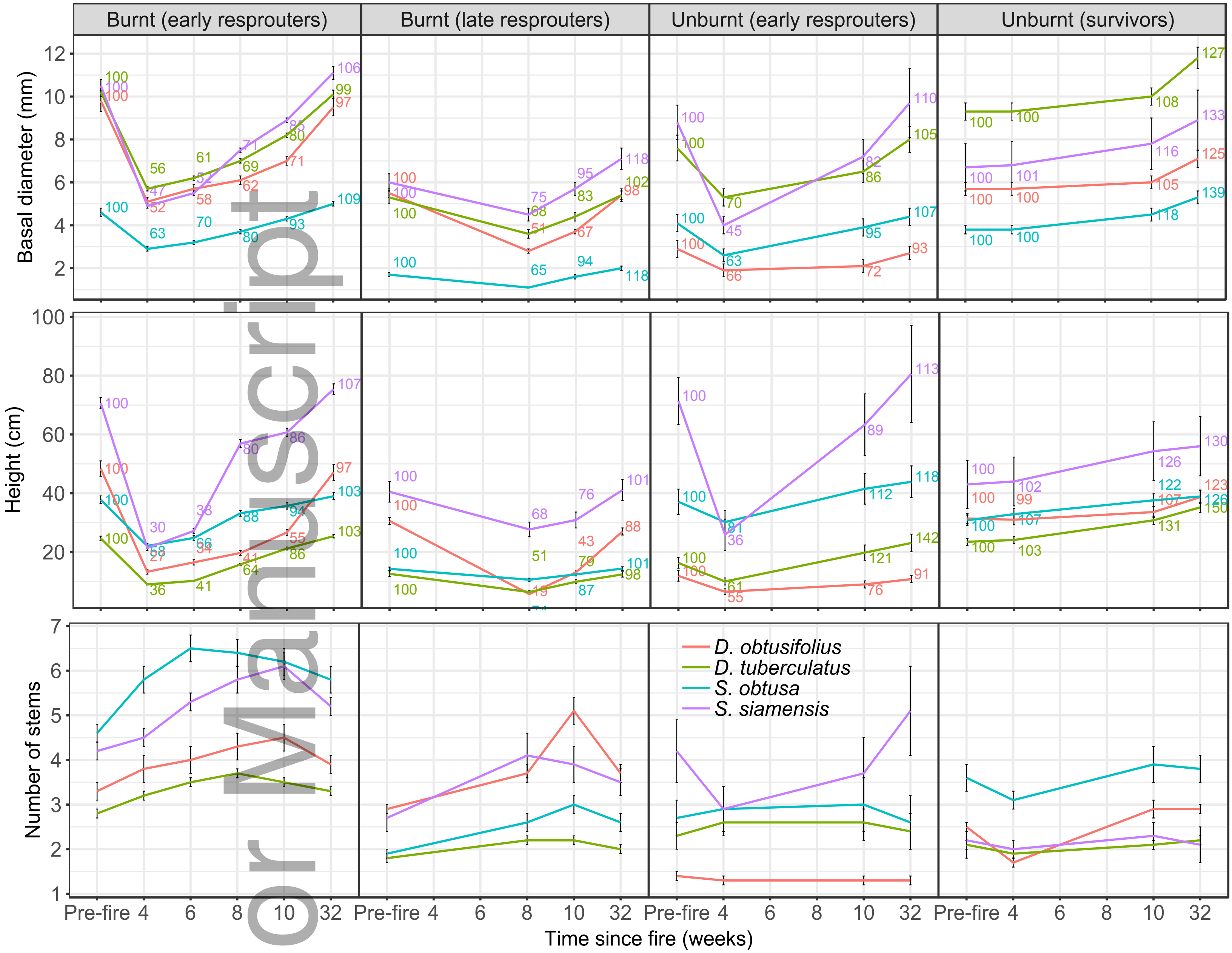
D. tuberculatus
S. obtusa
S. siamensis



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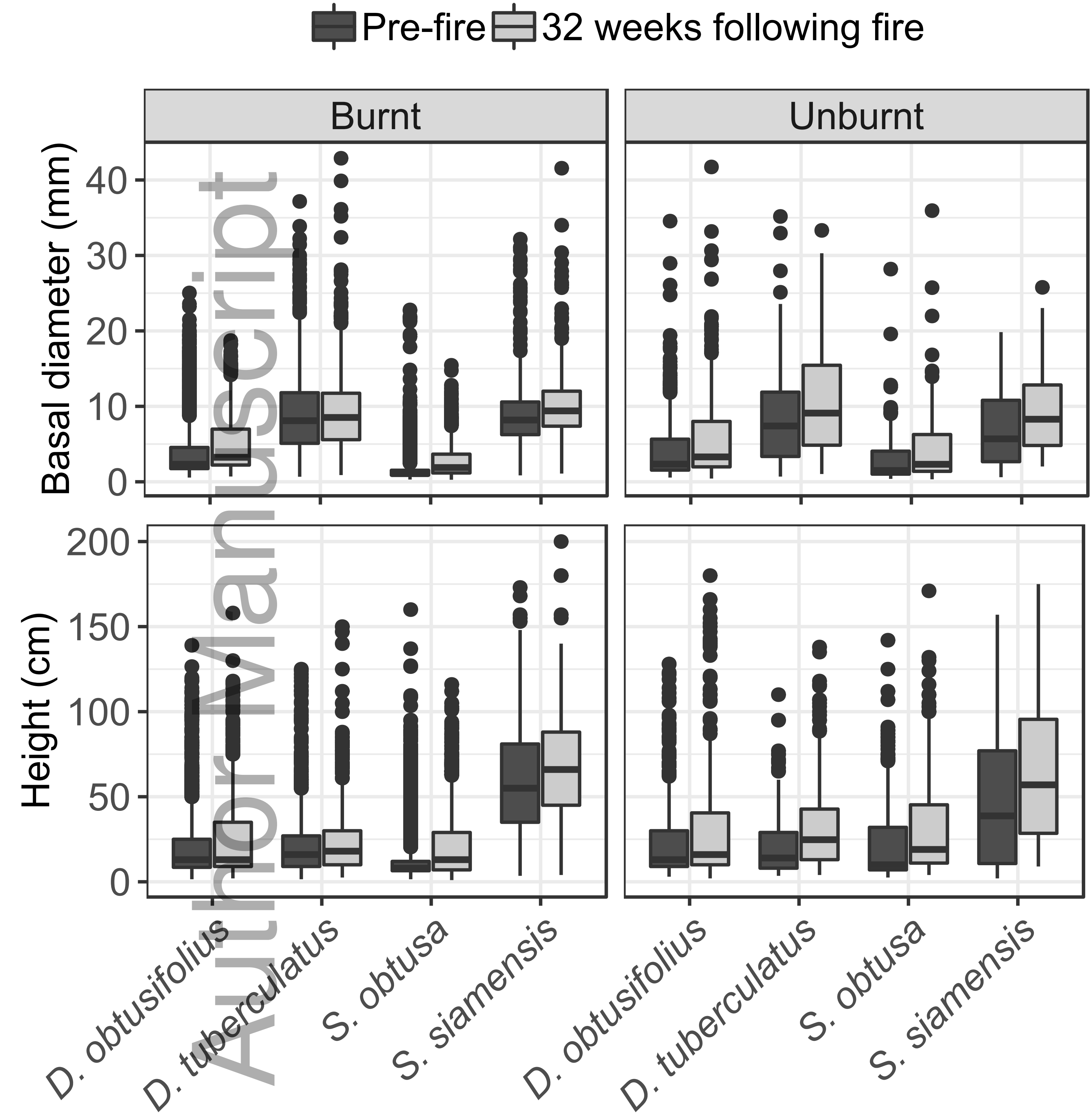

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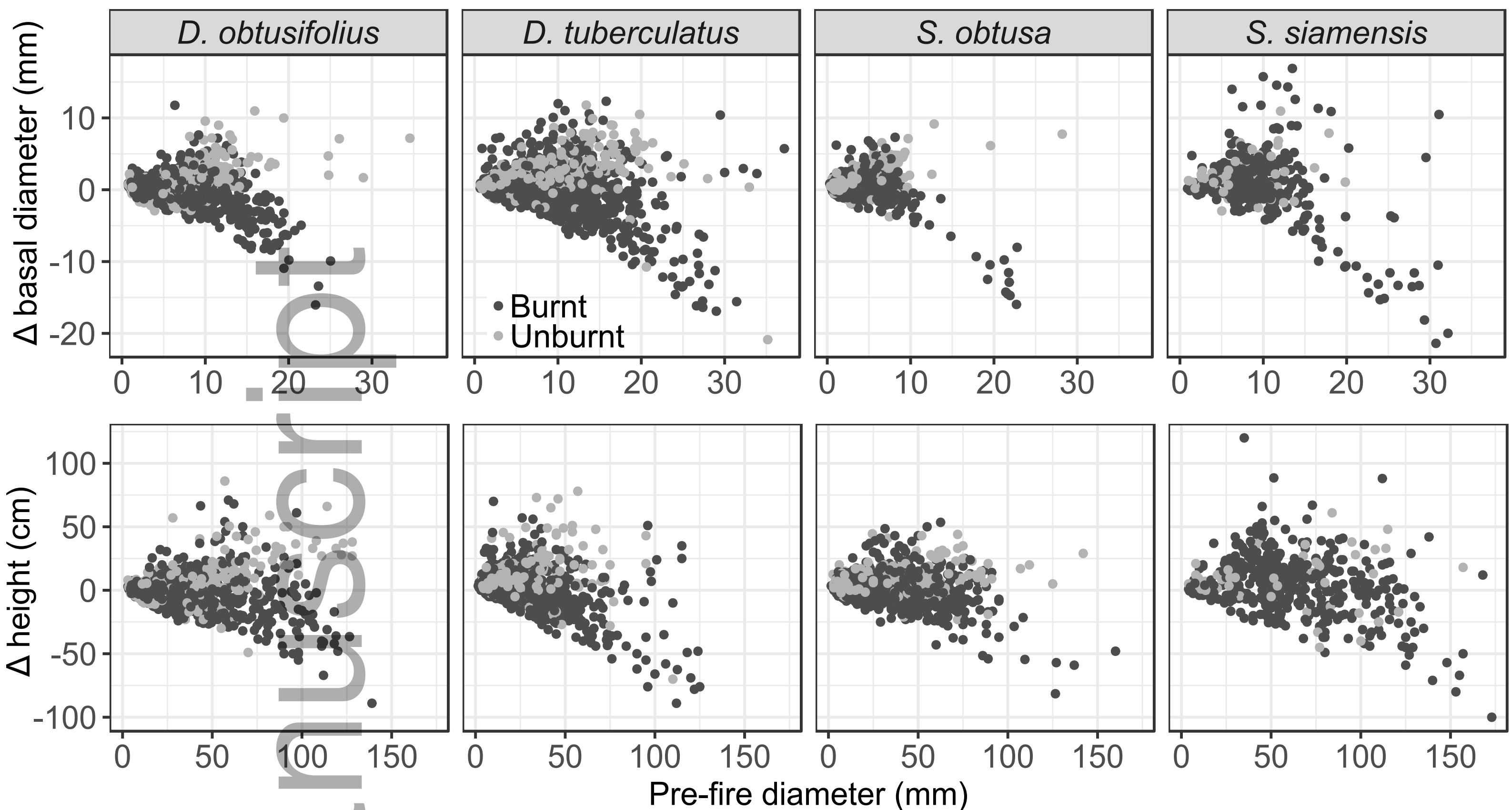

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