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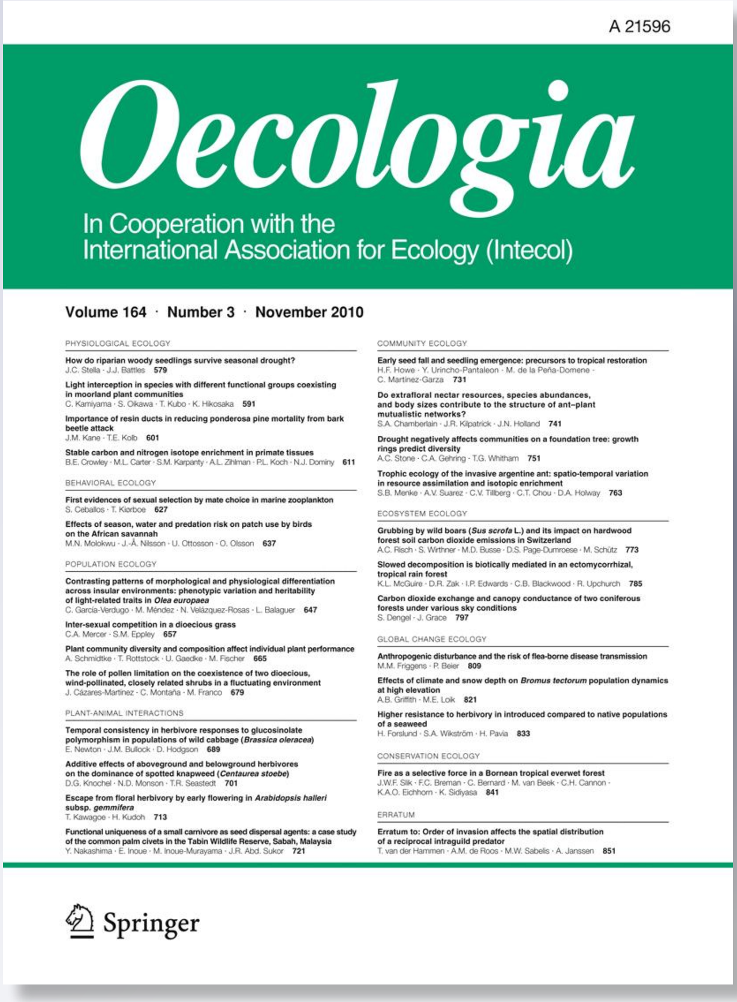

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CONSERVATION ECOLOGY - ORIGINAL PAPER

Fire as a selective force in a Bornean tropical everwet forest

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Abstract Tree species rarely exposed to burning, like in everwet tropical forests, are unlikely to be fire adapted. Therefore, one could hypothesize that these species are affected equally by burning and that tree abundance changes are linked solely to fire behavior. Alternatively, if species do react differentially to burning, abundance changes should be linked to tree habitat preference and morphology. Using tree inventories from old-growth and adjacent burned Bornean forest in combination with a database on tree morphology and habitat preference, we test these alternative hypotheses by (1) determining whether species specific abundance changes after fire differ significantly from equal change, and (2) whether observed abundance changes are linked to species morphology and habitat preference. We found that of 196 species tested, 125 species showed an abundance change significantly different from that expected under our null model of equal change. These abundance changes were significantly linked to both tree morphology and habitat preference. Abundance declines were associated with slope or ridge preference, thin barks, and limited seed dormancy. Abundance increases were associated with high light preference, small adult stature, light wood, large leaves, small seeds and long seed dormancy. While species habitat preference and morphology explained observed abundance increases well, abundance declines were only weakly associated with them ($R^2 \sim 0.09$). This suggests that most tree mortality was random and everwet tropical tree species are poorly fire adapted. As fire frequencies are increasing in the everwet tropics, this might eventually result in permanently altered species compositions and even species extinctions.

Keywords Fire mortality · Functional traits · Habitat niche · Life history · Tropical trees

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Introduction

Several studies have shown that undisturbed old-growth forests are difficult to burn due to their high air humidity and high moisture content of soil and litter, even after prolonged droughts (Uhl et al. 1988; Uhl and Kauffman 1990; Ray et al. 2005). For this reason, forest fires in the everwet tropics used to be a rare phenomenon, mostly occurring locally and at irregular intervals of several 100 years (Goldammer 1989; Cochrane 2003; Power et al. 2008). This has changed since the second half of the last century, when large tracts of old growth forest were opened up for logging, mining, infrastructure and agriculture (Bradshaw et al. 2009). Most tropical forests remaining today are either disturbed or fragmented and have become increasingly susceptible to droughts and fire (Uhl and Kauffman 1990; Cochrane et al. 1999; Siegert et al. 2001). Forest fires are now a common, large-scale and almost continuous phenomenon in most everwet tropical regions of the world. This is worrisome since it is questionable whether everwet tropical tree species that have rarely been exposed to fire in the past are adapted to cope with this new fire disturbance regime. At the same time, it offers an opportunity to investigate if forest fires affect tropical tree species abundances differentially, and if they do, how this is related to habitat preferences or plant functional traits. Insight into this might help us understand how tropical forests can evolve from one type into another under different scenarios of future climatic change and associated fire regimes.

Understanding the impact of fires on everwet tropical forests has become an important research topic during the last decades. Many studies have shown that fires can lead to dramatic and lasting changes in forest structure and tree species composition (Cochrane 2003; Barlow and Peres 2008; Slik et al. 2008). Generally, fire affects small diameter trees most, with tree mortality rates nearing 100% [diameter at breast height (dbh) <10 cm] (Uhl and Buschbacher 1985; Isichei et al. 1986; Woods 1989; Slik and Eichhorn 2003). This is linked to the strong relationship between tree diameter and bark thickness with thinner stems having thinner barks to protect them against the heat radiation generated by fire (Uhl and Kauffman 1990; Barlow et al. 2003; van Nieuwstadt and Sheil 2005; Michaletz and Johnson 2007). Presence of buttresses, resin and smooth barks can also increase tree fire mortality due to accumulation of litter fuel load between buttresses, flammability of resins, and a thinner isolating air boundary layer during fire exposure resulting in higher bark temperatures, respectively (Barlow et al. 2003). Next to these morphological factors, non-random spatial patterns of fire occurrence and intensity linked to fuel loads (Uhl and Kauffman 1990; Barlow et al. 2003), topography and soil/litter moisture (Uhl and Kauffman 1990; Slik and Eichhorn 2003; Nepstad et al. 2004; Ray et al. 2005), and canopy openness (Uhl and Buschbacher 1985; Woods 1989) have been shown to affect tree fire mortality rates differentially throughout the landscape.

Tree species recovery and community compositional changes after fire are also strongly linked to survival and colonization patterns. Several studies have shown that resprouting and emergence from the soil seed bank can be important mechanisms by which tree species survive or even profit from fires (Riswan and Yusuf 1986; Isichei et al. 1986; de Rouw and van Oers 1988; Marod et al. 2002; Fensham et al. 2003; Vesk and Westoby 2004; Baker et al. 2008), while good dispersal ability in combination with early reproductive maturity form additional strategies enabling tree species to cope with a regular fire regime (Uhl et al. 1981; Hoffmann et al. 2003; Muller et al. 2007).

Fire studies in the everwet tropics have mainly focused on general trends in tree fire mortality and survival, indiscriminate of species identities, or when they did focus on species-specific survival rates, included only a few species. Therefore, it remains unclear how these general findings translate to species-specific abundance changes, and thus if and how fires work as a selective force in everwet tropical forests. If fire affects all species equal, then fire damage will be largely driven by spatial patterns in fire behavior. However, if species are affected differentially, fire damage will result in more complicated spatial patterns based on interactions between fire behavior, tree species habitat preferences and tree morphology. To resolve this issue, we tested whether (1) changes in species abundance after fire are dependent on species identity, and (2) if so whether these changes are related to tree morphological traits and habitat preferences.

Materials and methods

Study site

The Sungai Wain Protection Forest is located ca. 15 km north-west of the city of Balikpapan, East Kalimantan, Indonesia (Fig. 1). Two-thirds of this forest (ca. 8,000 ha) was burned in April 1998 after a prolonged drought that was associated with a severe El Nino Southern Oscillation (ENSO) event, while a ca. 4,000-ha core area was saved from fire by man-made fire breaks. The fires were low intensity surface fires that slowly moved through the area mainly fuelled by the thin litter layer. These fires caused significant tree mortality especially in the small diameter classes (dbh < 10 cm) (Slik and Eichhorn 2003; van Nieuwstadt and Sheil 2005). The area receives a mean of ~2,400 mm precipitation annually, with rainfall exceeding evaporation in all months (Walsh 1996). Soils are relatively

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Fig. 1 Map indicating the location of the research area sites in Borneo (*arrow* in *left* map). Two 450-ha plots were established in unburned (*0*) and adjacent burned (*1*) forest (*right* map)

poor and sandy and the topography covers an elevation gradient of 10–120 m above sea level. The area includes freshwater swamps, coastal tidal areas, periodically inundated river valleys and low hill ridges. The vegetation composition and forest structure is typical for lowland coastal forests in eastern Borneo, with forests within a 30-km radius of the research area showing high floristic and structural similarity (Slik et al. 2003; Eichhorn 2006; Slik et al. 2009; Slik et al. 2010).

Tree abundance data

Tree abundance data were taken from a large field inventory carried out 2 years after the 1998 fires in the Sungai Wain Protection Forest (Eichhorn 2006). The inventory was conducted in two north–nouth oriented 1.5 × 3.0 km (450-ha) squares, one in burned old-growth and one in adjacent unburned old-growth forest (Fig. 1). Each square contained 80 randomly distributed plots of 10 × 20 m (0.02 ha). Within each plot, all live trees taller than 1.3 m were identified [voucher specimens deposited in the Nationaal Herbarium Nederland, Leiden University, The Netherlands ([NHN-L)] and their dbh measured. A total of 28,388 individuals were found belonging to 695 (morpho)-species, representing about one-third of the known tree species in the Sungai Wain Protection Forest (http:\\www.nationaalherbarium.nl/sungaiwain). From these, we excluded species with less than 10 individuals and morpho-species (499 species excluded of which 235 were morpho-species, 41 of which had more than 10 individuals) resulting in a total of 196 species used in the analyses (Appendix 1, see supplementary material). Unfortunately, no pre-fire data was available for the burned forest square; however, given the relatively uniform landscape, close proximity of the two plots, our use of only common species and limited floristic variability observed within a 30-km radius of our study site (Slik et al. 2003; Eichhorn 2006), we assume that both plots had comparable species composition and abundances.

Detecting significant species specific abundance changes after fire

For the 196 species, we found 10,723 (76.6%) individuals in the unburned versus 3,283 (23.4%) in the burned plots. We used this overall abundance difference between unburned and burned forest to calculate expected abundances for each species in the burned forest. For each species, we tested whether observed abundance in burned forest was significantly lower or higher than the expected abundance using a one-tailed Fisher's Exact test. Unlike the Chi-square test, the Fisher's Exact test can be reliably applied with categories containing less than five individuals. Even when abundance change after fire would be random for all species, one would expect to find 10 species with a significantly larger or lower abundance change than expected using a 0.05 probability (p) value (0.05 × 196 species). To determine whether our observed number of species with a significant abundance deviation differed from the expected number of 10, we again performed a Fisher's Exact test.

Ranking species according to abundance change

We used three abundance change measures: (1) 'absolute' which ranked species from low to high according to difference between observed and expected number of individuals in burned forest; (2) 'relative' which ranked species from low to high according to percentage change between observed and expected number of individuals in burned forest; and (3) 'combined' which ranked species from low to high based on the average of their absolute and relative abundance rank. The absolute measure gives a direct indication of the number of individuals lost or gained per species and therefore gives more weight to species with high pre-fire abundance since more abundant species can lose more individuals. The relative measure, on the other hand, gives more weight to less abundant species since loss or gain of an individual in a rare species counts for more than a single loss or gain in a common species. The combined abundance measure should give a more balanced indication of abundance change since it equalizes the overweighting of common and rare species.

Species habitat preferences and morphological attributes

Species habitat preferences were determined using a large database of tree inventories including 26,604 individual trees belonging to 1,469 taxa, of which 989 were identified to species level (including all 196 species used in our analyses). These inventories took place between 1997 and 2005 in small 10 × 10 m (0.01-ha) plots and were spread over a large portion of East Kalimantan Province. They included old-growth forests, logged forests, burned forests, logged

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and burned forests, and logged and thinned forests within an altitude range of 10–1,200 m. The following habitat variables were determined for each species in this data set: (1) the median canopy openness (determined from hemispherical canopy photographs taken in the center of each 0.01-ha plot) under which individuals were found to grow; (2) the median slope (determined with a clinometer for each 0.01-ha plot) on which individuals were found to grow; (3) the topographical class [alluvial (swamps, river valleys, flood plains); hillside (sloped area between valleys and hill tops); ridge (hill tops)], based on the percentage of individuals found growing in each topographic class; and (4) soil texture (clay, silt, fine sand, sand, coarse sand), based on the percentage of individuals found growing in each soil texture class.

Morphological variables and elevation preference for each species were determined from a minimum of ten herbarium specimens per species in the NHN-L, and included: (1) minimum reproductive diameter (determined by ranking the dbh values scored from herbarium labels of fertile specimens from small to large, plotting them in a scattergraph ($Y = \text{dbh}$; $X = \text{rank}$), fitting an exponential function through the graph, and scoring the Y-intercept of this function as the minimum reproductive dbh); (2) maximum adult diameter (determined in the same way as minimum reproductive diameter, but this time with the dbh values ranked from high to low); (3) maximum adult height (determined in the same way as maximum diameter, but then using estimated tree heights); (4) mean elevation above sea level; (5) maximum elevation above sea level; (6) leaf size based on the mean of length multiplied by width values; (7) leaf shape based on the mean length divided by width values; (8) fruit size based on the mean maximum fruit length; (9) seed size based on the mean maximum seed diameter; and (10) flower size based on the mean maximum flower diameter.

We also determined mean oven-dry wood density of each species based on reported values in the literature (Oey 1990; Suzuki 1999; Osunkoya et al. 2007), or when a species had no recorded wood density, from the genus average (sensu Slik 2006). Median population bark thickness in old growth forest was determined for each species using the individuals found in the unburned forest plot. This was based on a diameter–bark thickness relationship measured in the Sungai Wain Protection Forest by van Nieuwstadt (2002): bark thickness $= 10^{[-1.21 + 0.669\text{LOG10(dbh)}]}$. van Nieuwstadt (2002) also presented a species sprouting frequency equation (percentage sprouting = 37.1–38.9 × oven dry wood density), but since this relationship depends completely on the wood density values already included in our study, we did not use it here. As an indication of seed dormancy capacity of the tree species in our study, we used the maximum observed species germination times recorded by Ng (1991). If a tree species was not treated by Ng (1991), we used the average maximum germination time of the genus to which it belonged. If a genus was not present in Ng (1991), we used the average maximum germination time of the phylogenetically closest related genus for which data was available.

Variable selection for final analyses

Our selection of morphological and habitat variables was based on the assumption that they were related to tree fire mortality, survival and/or colonization patterns. However, for our final analyses, we wanted to exclude redundant variables, i.e. variables that were strongly correlated to other variables (correlation coefficient >0.7). To do that, we performed a Pearson's Rank correlation test for all pair-wise combinations of variables (Appendix 2, see supplementary material). This showed that the following variables were highly correlated: (1) 'Alluvial' and 'Ridge', (2) all 'Soil Texture' variables, (3) 'Reproductive dbh', 'Maximum dbh' and 'Maximum height', (4) 'Mean elevation' and 'Maximum elevation', and (5) 'Fruit size' and 'Seed size'. Therefore, we excluded the following variables from the final analyses: (1) 'Ridge', (2) 'Clay', 'Fine sand', 'Sand' and 'coarse sand', (3) 'Reproductive dbh' and 'Maximum height', (4) 'Maximum elevation', and (5) 'Fruit size'. This left 14 variables for final analysis.

Explaining species abundance changes

We used Akaike's information criterion (AIC) to select the variables that best explained the observed species abundance changes using the Spatial Analysis in Macroecology (SAM) software developed by Rangel et al. (2006). This software calculates multiple regression models for all possible combinations of variables, i.e. for our 14 final variables there were 16,383 possible combinations, and then ranks these models according to their AIC score. AIC selects models based on a compromise between least number of variables included, highest possible explanatory power and lowest residual variation. This analysis was performed to explain 'Absolute abundance change', 'Relative abundance change' and the 'Combined abundance change' for: (1) all species, (2) species that had declined in abundance after fire, and (3) species that had increased in abundance after fire. We did this to be able to identify not only the processes that drive the overall abundance change of the tree population after fire but also the specific ones associated with tree species abundance declines and increases.

Testing for phylogenetic autocorrelation

An important aspect of species-specific analyses is the fact that due to their evolutionary descent, species cannot

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automatically be assumed to be independent sample units. Since independence of sample units is an important prerequisite of most statistical tests (dependence leads to inflated degrees of freedom in statistical testing and thus *p* values that cannot be trusted), it is important to check whether the difference between the observed and predicted values of models (residuals) are independent of species phylogenetic relationships. To test for this, we used a phylogenetic tree that was resolved up to genus level for most Bornean tree genera (Slik et al. 2009) as input phylogeny in the program PHYLOMATIC (http://www.phylodiversity.net/phylomatic/), and then pruned it down to contain only the genera present in our dataset (Appendix 3, see supplementary material). Using the BLADJ function in PHYLOCOM (Webb et al. 2008) in combination with estimated family ages (Wikstrom et al. 2001), we dated this phylogeny. We then calculated the phylogenetic distance in millions of years ('phydist' in PHYLOCOM) between all possible pairs of species in this phylogeny. The resulting matrix was entered in a Principal Coordinate Analysis (PCO) to summarize phylogenetic patterns along the main PCO axes. The first PCO axis separated species from 'primitive' to 'advanced', while the second axis differentiated between the Eurosid1 and 2 clades. We used the coordinate of each species on the first two PCO axes as the values indicating their phylogenetic position in relation to all other species. This data was used to calculate Moran's I values for our model residuals in the program SAM (with *X* containing PCO axis 1 coordinate and *Y* containing the PCO axis 2 coordinate of each species). In this way, we were able to detect presence or absence of residual phylogenetic autocorrelation in our final models.

Results

Of the 196 tree species tested, 150 had lower than expected abundance while 46 had higher than expected abundance after fire (Fig. 2; Appendix 1, see supplementary material). For 125 of the 196 species, the observed abundance in burned forest was significantly larger or lower than expected, which was significantly higher (one-tailed Fisher's Exact test $p < 0.0001$) than the expected value of 10 species if abundance change across species would have been equal (using a probability value of 0.05).

Tree morphology and habitat preference had a significant effect on species abundance changes after fire (Table 1). The three best models (for absolute, relative and combined abundance change) explained between 26.6 and 34.4% of data variance when all species were analyzed simultaneously. This analysis showed that a mix of tree species morphological characteristics and habitat preferences influenced their abundance change after fire. Tree species with heavy wood, large seeds, short seed dormancy, preferring hillsides and/or closed canopy were affected most adversely by fire, while tree species with light wood, small seeds, long seed dormancy, preferring alluvial sites and/or an open canopy were less affected or increased in abundance after fire. There was high agreement among selected variables for the three abundance change measures, with the only exception being seed dormancy, which was only important in explaining absolute abundance changes.

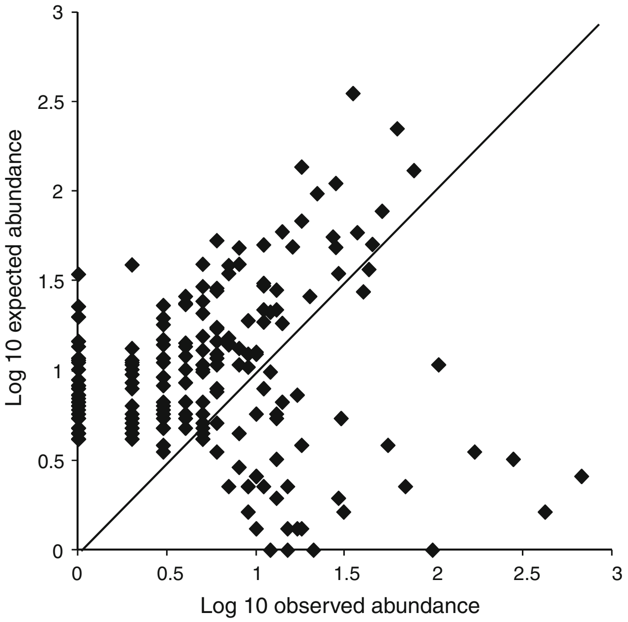

Fig. 2 Plot of observed versus expected species abundance in burned forest. *Line* indicates no change; points *below line* are species that increased in abundance; points *above line* are species that decreased in abundance after fire

Amount of variance explained by the models decreased markedly (between 6.2 and 11.3%) when only species were analyzed that had declined after fire. The most important variables responsible for abundances change in declining species after fire were: topographic habitat preference, bark thickness, and seed dormancy. Species with a preference for alluvial sites, having a population structure consisting of mostly large diameter trees with thick barks and/or long seed dormancy, showed limited abundance decline after fire, while tree species growing on hillsides and ridges, having a population structure consisting of mainly small trees with thin barks and/or short seed dormancy, declined the most. Again, there was high agreement among selected variables for the three abundance change measures, with seed dormancy as an exception.

The models were able to explain high levels of data variance (between 32.0 and 45.9%) when species that increased after fire were analyzed. The most important variables were canopy openness preference, maximum adult diameter,

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Table 1 Modeling results (R^2-adjusted, F-ratio, P value, n, and presence of phylogenetic autocorrelation of residuals) for the best model selected for: (1) all species, (2) species that declined in abundance after fire, and (3) species that increased in abundance after fire. Importance of variables (% presence in models with a delta-AIC score <2) and direction of correlation with abundance change are also added. Variables selected in the single best model (lowest AIC-score) are underlined. Total number of models with delta-AIC score ≤2 indicated in the last table row

	All species			Decline species			Increase species		
	Absolute	Relative	Combined	Absolute	Relative	Combined	Absolute	Relative	Combined
R^2 adjust	31.7	26.6	34.4	11.3	6.2	9.4	32.0	45.9	41.8
F ratio	15.6	14.6	20.0	6.6	4.8	7.6	7.1	12.5	8.2
P	<0.001	<0.001	<0.001	<0.001	0.009	<0.001	<0.001	<0.001	<0.001
n	196	196	196	150	150	150	46	46	46
Phylo-autocor.	No	No	Limited	No	No	No	No	No	No
Variable importance									
Canopy openness	100.0 (+)	100.0 (+)	100.0 (+)	46.7 (+)	0.0	21.7 (+)	90.0 (+)	100.0 (+)	100.0 (+)
Slope	5.3 (+)	0.0	0.0	0.0	15.4 (−)	4.3 (−)	30.0 (−)	0.0	0.0
Alluvial pref.	100.0 (+)	62.5 (+)	100.0 (+)	100.0 (+)	7.7 (+)	60.9 (+)	50.0 (−)	0.0	22.2 (−)
Hillside pref.	94.7 (−)	100.0 (−)	100.0 (−)	20.0 (−)	76.9 (−)	56.5 (−)	0.0	0.0	0.0
Silt pref.	31.6 (+)	0.0	7.7 (+)	26.7 (+)	15.4 (−)	4.3 (+)	0.0	0.0	0.0
Dbh max.	26.3 (−)	18.8 (−)	23.1 (−)	6.7 (−)	0.0	0.0	90.0 (−)	50.0 (−)	100.0 (−)
Elevation	5.3 (+)	0.0	0.0 (+)	0.0	7.7 (−)	4.3 (−)	0.0	16.7 (−)	22.2 (−)
Wood density	100.0 (−)	100.0 (−)	100.0 (−)	0.0	7.7 (−)	4.3 (−)	0.0	66.7 (−)	11.1 (−)
Leaf size	5.3 (+)	25.0 (+)	23.1 (+)	20.0 (−)	7.7 (+)	4.3 (−)	60.0 (+)	33.3 (+)	44.4 (+)
Leaf shape	5.3 (−)	0.0	7.7 (−)	0.0	7.7 (+)	17.4 (+)	0.0	0.0	0.0
Seed size	68.4 (−)	43.8 (−)	61.5 (−)	13.3 (−)	0.0	0.0	20.0 (−)	100.0 (−)	55.6 (−)
Flower size	10.5 (−)	18.8 (−)	15.4 (−)	13.3 (−)	7.7 (−)	13.0 (−)	0.0	0.0	0.0
Bark thickness	10.5 (+)	6.3 (+)	7.7 (+)	100.0 (+)	100.0 (+)	100.0 (+)	0.0	0.0	0.0
Seed dormancy	89.5 (+)	6.3 (−)	7.7 (+)	100.0 (+)	0.0	13.0 (+)	0.0 (+)	0.0	0.0
Model nr.	19	16	13	15	13	23	10	6	9

wood density, leaf size and seed size. Species preferring an open canopy, having a small adult stature, light weighted wood, large leaves and/or small seeds increased strongly after fire. Models for absolute, relative and combined abundance change largely agreed on the responsible variables with the exception of wood density, which was only important for explaining changes in relative abundance after fire.

We detected only one case of phylogenetic autocorrelation in the model residuals (Appendix 4, see supplementary material). However, this was limited to one phylogenetic distance class with a very low value of autocorrelation (Moran's I of −0.065, on a scale running from −1 to +1), and thus did not affect model statistics seriously.

Discussion

Our analysis shows that fire in an everwet tropical forest can affect abundances of co-existing species differentially. This means that, even after a single low intensity surface fire, species diversity and composition patterns will be severely altered. This change was related both to species habitat preferences and species morphological traits. Topographic position, which is strongly linked to soil moisture content during drought (Daws et al. 2002; Gibbons and Newbery 2002) and the associated fire risk and intensity (Slik and Eichhorn 2003), was a major factor affecting tree fire mortality, recruitment and survival, with tree species preferring hillsides and ridges generally showing higher abundance declines than tree species preferring alluvial sites. It was already known for our study area that lowest tree mortality occurred in river valleys and swamps, resulting in a patchily connected network of forest that was relatively unaffected by fire (van Nieuwstadt 2002; Slik and Eichhorn 2003; Eichhorn 2006), but our study shows that this pattern directly translates into changes in species composition of burned forest due to species-specific habitat preferences. This means that the previously suggested importance of the remaining unaffected alluvial forest patches in the recovery of burned forest might be limited due to the fact that the species found there might not be able to perform well on hillsides and ridges. Even if they do manage to disperse and establish successfully onto hillsides

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and ridges, the species composition will remain different from that of the pre-fire forest.

Species functional traits were also important determinants of tree species abundance changes after fire. Our analysis shows that median population bark thickness and seed dormancy capacity are two main determinants of species abundance declines after fire. Since bark thickness was calculated based on a correlation with stem dbh, this indicates that species characterized by a large standing stock of small diameter trees were affected most negatively by fire. These are generally late successional understorey species and canopy tree species with large standing stocks of saplings. These two species groups usually possess low seed dormancy capacity, which might explain the observed negative correlation between seed dormancy length and species abundance decline. Another reason why seed dormancy length was correlated negatively with species abundance decline might be related to the fact that species with seed dormancy posses a seed bank in the soil. Since our data were collected 2 years after the fire, this might already have included individuals that germinated from this soil seed bank thus resulting in less severe abundance declines after fire for species possessing seed dormancy.

Species that increased after fire were characterized by high light preference, small stature, low wood density, large leaves and/or small seeds. These characteristics are typical for early successional tree species (Swaine and Whitmore 1988), although wood density has also been shown to correlate negatively with species sprouting capacity (van Nieuwstadt 2002), suggesting that increased sprouting capacity may also explain the observed abundance increases. The burned forest was indeed strongly dominated by several pioneer tree species, which is a common pattern found in burned forests across the tropics (Isichei et al. 1986; Barlow and Peres 2008; Slik et al. 2008). Many of the species that increased in abundance after fire were very rare or even absent in the unburned forest, meaning that they either dispersed into the burned forest over distances of several kilometers or were already present in the soil seed bank. A study by van Nieuwstadt (2002) did find many of the pioneer tree species germinating from soil samples collected in the unburned forest a few months after the 1998 fires (thus before any serious seed input from the burned forest could have altered the seed composition of his soil samples), suggesting that the soil seed bank may have played a role in the establishment of these species. This would be in accordance with pioneer establishment in other tropical forests (Garwood 1989).

It is noteworthy that our models were only able to explain ~9% of data variance in tree species that declined in abundance after fire suggesting that most of the fire mortality was random and that selective species extinctions will only occur after repeated burning. However, the amount of explained data variance might increase by inclusion of additional factors which were shown to be important in the Neotropics but for which we did not have enough data (Barlow et al. 2003). These are the presence of resin and buttresses, sprouting capacity, bark structure, mycorrhizal associations, and distribution of fire fuel load in the forest. Additionally, data on two main fire survival characteristics was lacking, namely species-specific sprouting capacity and bark thickness. Additional research will have to be carried out to measure these factors in the field to determine how this will affect the results of our analyses.

The changes in species-specific abundances and associated shifts in species composition in everwet forests after fire contrast strongly with observations from the more seasonal forests of continental southeast Asia. In these seasonal forests, fire had a limited impact on species diversity and composition and most species seemed to be fire adapted, possessing relatively high sprouting rates and thick barks (Baker et al. 2008). Traditionally, the floristic transition from everwet to seasonal tropical forests has been ascribed to progressively increasing dry season length and resulting drought stress (Hely et al. 2006; ter Steege et al. 2006; Slik et al. 2009). However, since dry season length also affects fire risk and frequency (Van der Werf et al. 2008), part of this floristic shift might be caused by the selective pressure of forest fires. This would mirror the transition from tropical seasonal forest to savannah where fire has already been shown to be a main driving factor of species compositional and forest structural transition, next to the precipitation regime (Hoffmann et al. 2003; Banfai and Bowman 2005; Beerling and Osborne 2006).

In principal, it is possible to tease apart the effects of precipitation and fire on tree species composition and forest structure since droughts affect tree composition differently than fires. Droughts mostly affect large-statured upper canopy and emergent evergreen trees with relatively low wood densities (Slik 2004; van Nieuwstadt and Sheil 2005). Therefore, decreasing amounts of rainfall and longer dry season length should lead to forests dominated by relatively short-statured heavy wooded and/or deciduous tree species, which corresponds to observations along increasing dry season length gradients in the Neotropics (Malhi et al. 2006). Fire on the other hand mostly affects small trees with thin barks, heavy wood, low sprouting capacity, large seeds with short seed dormancy and late reproductive maturity (Barlow et al. 2003; Slik and Eichhorn 2003; van Nieuwstadt and Sheil 2005). Therefore, forests that are regularly burned should become dominated by trees with thick barks, high sprouting capacity, well-developed seed dormancy, light wood, small seeds and/or early reproductive age, such as are found in the seasonal forests of mainland Southeast Asia (Baker et al. 2008). The combined effect of drought and fire could result in a mosaic of forest types

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differing in species composition and structure depending on regularity and intensity of fires and droughts. This corresponds to the co-occurrence and patchy distribution of different forest types (seasonal dry evergreen, mixed deciduous, deciduous dipterocarp and many intermediates) in seasonal southeast Asia (Zhu et al. 2006; Baker et al. 2008).

Conclusions

Fire did affect species abundances differentially, and this change was linked to species habitat preferences and morphology, although only ~9% of species abundance declines could be explained in this manner. This indicates that most tree mortality due to fire was random, although it cannot be ruled out that inclusion of more species attributes (like sprouting capacity and bark thickness) could increase the amount of explained abundance decline. Based on our current analysis, it seems likely that several fires are needed to lead to selective species extinctions. On the other hand, our analysis very clearly identified species characteristics associated with abundance increases after fire. These were mostly morphological traits associated with early successional life history strategies caused by the strong increase of pioneer species after fire. Overall, our analysis indicates that everwet tropical tree species are not well adapted to fire. The increase in fire frequency in recent decades might therefore pose a serious threat to these forests, with decreasing tree diversity and species compositions starting to resemble those of Asia's seasonal tropical forests.

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