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Tree mortality following ENSO-associated fires and drought in lowland rain forests of Eastern Nicaragua

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ABSTRACT

Occurrence of fires is an unusual event in many tropical *terra firma* rain forests, in particular those in Mesoamerica. As a result of the unusually intense ENSO event of 1998/1999, these forests were subjected to a prolonged drought that favored the propagation of extensive fires. In the lowland rain forests of the Atlantic Coast of Nicaragua, fires were mostly low-intensity leaf litter fires, but they produced high tree mortality. Data from 5 to 17 years of study of permanent plots/transects from four sites were used to investigate whether survival following the ENSO drought episode and subsequent fires may be affected by factors such as successional status, tree size, taxonomic identity or growth rate. The study included two sites that burned in their entirety, one that had only part of its area burned and a fourth site that was not affected by fire. Overall, tree survival was lower in burned plots, and remained low in those plots for at least 2 years after fires, especially among pioneer and mature forest species. Mortality experience between burnt and unburned plots differed widely among the 15 most abundant species. The 38 most abundant species were grouped into five guilds corresponding to their ecological successional status: (1) pioneers; (2) subcanopy/understory heliophiles; (3) canopy heliophiles; (4) subcanopy mature forest species; (5) canopy mature forest species. All guilds experienced significantly lower survival in plots that burned in mortality among guilds were between significant differences. The only the canopy mature forest species and the pioneers, which had the highest mortality. Two years after fire, survival remained significantly lower in burnt plots than in plots that had not burned, but the pattern of mortality was quite different. Both mature forest species guilds had significantly higher mortality than heliophile guilds. Tree size had an overall significant positive effect on survival after fires particularly among subcanopy and canopy mature forest species guilds. However, in unburned sites, survival was negatively correlated to tree size in mature forest guilds. While relative growth rate had no overall significant effect in plots that burned, faster growth was positively correlated with survival in particular guilds such as in pioneers and canopy heliophiles. Delayed mortality increased with relative growth rate for pioneers but decreased for subcanopy heliophiles. The effect of the ENSO event drought resulted in a significantly reduced overall survival caused by high mortality of pioneers, compared to non-drought years and to other guilds, but non-significant differences in post-drought survival were apparent among the remaining guilds. Individual tree basal area was positively correlated with survival given drought, overall, but particularly in pioneers and mature forest canopy species. Contrary to hurricanes, the delayed mortality and overall damage caused by fires is not conducive to maintaining the structure, diversity and species composition of these forests.

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1. Introduction

Historically, tropical rain forests, including those in Mesoamerica, have been subjected to occasional fires before human presence.

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Charcoal deposits over a wide altitudinal gradient indicate recurrent and recent fire events in many (if not most) of the world's wet tropics (Goldammer and Seibert, 1989; Clark and Robinson, 1993; Titiz and Sanford, 2007). Rain forests such as those in Borneo, and to a lesser extent in the Amazon Basin, have a history of recurrent fires, with or without human intervention. Grazing and logging render uncommonly dry conditions at the edges and within intervened rain forests, which has favored fires in those regions as well as Northern Australian rain forests (Uhl and

Kauffman, 1990; Goldammer, 1993; Holdsworth and Uhl, 1997; Nepstad et al., 1999; Cleary and Priadjati, 2005; Simbolon et al., 2005; van Nieuwstadt and Sheil, 2005). Recurrent fires may not have been as common for the Mesoamerican humid tropics, but a combination of factors may certainly enhance the probability of fires occurring in ecosystems otherwise regarded as unburnable (Uhl et al., 1988; Goldammer and Seibert, 1990; Kauffman and Uhl, 1990; Holdsworth and Uhl, 1997; Cochrane, 2003).

In addition to burning directly induced by humans, fires in tropical forests are also currently experiencing a climate forcing due to changing conditions including increased evapotranspiration, greater risk of drought, and, in the Caribbean Basin, a tendency toward lesser precipitation (Bates et al., 2008; Solomon et al., 2007). These climate changes lead to prolonged dry seasons and more frequent and intense droughts. Another factor that may play yet a more important role in the occurrence of rain forests fire in most of Mesoamerica, and probably most of the Neotropics, is the fact that these forests have become more fragmented, consisting of smaller patches surrounded by a human-managed matrix. These agricultural activities range from low intensity cattle pastures to migratory slash and burn agriculture under different forms of production and management (Perfecto and Vandermeer, 2010). These systems have in common that they are all established or managed through burning (Cochrane, 2001, 2003; Cochrane and Laurance, 2002). Activities that favor open canopies increase the fire-prone landscape—rain forest ecotone conditions, so fires often penetrate into the contiguous forested areas (Holdsworth and Uhl, 1997; Cochrane, 2003; van Nieuwstadt and Sheil, 2005; Balch et al., 2009). Yearly fires end up carving off a few meters of the forest edge at a time. Although humidity inside the forest prevents further penetration of fires (Uhl and Kauffman, 1990; Goldammer, 1993), when forest edges become exposed to drier conditions and pressure from repeated burning, their species composition may change and become more prone to ignite (Barlow and Peres, 2006, 2008). All of the above, combined with the prolonged drought produced by an exceptionally intense ENSO, made these otherwise very humid ecosystems rather combustible, leading to the fires that swept throughout the humid tropics, worldwide, during the 1997–1998 dry season (Stolle and Tomich, 1999; Siegert et al., 2001; Barlow and Peres, 2003; Slik and Eichhorn, 2003; Slik, 2004; Cleary and Priadjati, 2005; van Nieuwstadt and Sheil, 2005).

Fires as widespread as these may have a historical precedent, but contrary to the more common disturbance of intense storms, they are not likely to be part of the natural dynamics of Central American rain forests. Burning therefore cannot be regarded as the kind of intermediate disturbance (*sensu* Connell, 1978; Huston, 1979) that maintains forest biodiversity. In addition, the effects of fires on tropical rain forests are expected to be long term, hampering their regeneration toward the original floristic composition (Uhl and Kauffman, 1990; Cochrane, 2003).

Studies of fire in tropical rain forests have largely focused on fire regime and vegetation dynamics, often describing this ecosystem as presenting low resilience to fire (Lloret and Zedler, 2009) due to the vulnerability to low-heat fires of many of its species (Pinard et al., 1999; Eriksson et al., 2003; Slik, 2004; Slik et al., 2008). This vulnerability could be due in part to insufficient protection by its bark (Pinard et al., 1999; van Nieuwstadt, 2002; Eriksson et al., 2003; Cleary and Priadjati, 2005; Baker et al., 2008; Slik et al., 2010) or to the proximity of their root systems to the soil surface (Montoya, 2011). Some of these species are dominant in the mature stages (Slik et al., 2002; Cleary and Priadjati, 2005), but an analysis of the highly diverse plant community assemblage of such ecosystems requires a detailed assessment of the individual species responses to fire as well as to drought (Slik, 2004; Barlow et al., 2003b; Balch et al., 2011). This response may be related to the successional status of the different taxa, especially for those

in which size distribution may be skewed toward certain size classes. Recent research has highlighted that stochastic processes are likely to contribute more to the community assemblage of early successional stages than to that of later stages when competitive interactions tend to become more intense (Stokes and Archer, 2010). The studies that documented the regeneration of rain forest in the southern Caribbean Coast of Nicaragua after Hurricane Joan of 1988 showed that the effect on the tree community is irrespective of individuals' taxonomic identity (Vandermeer et al., 1990, 1996; Yih et al., 1991; Ruiz et al., 2010). This suggests that forest dynamics may be determined by neutral, stochastic processes that include response to disturbance and the creation of light gaps (Hubbell and Foster, 1986; Hubbell, 1999, 2001; Hubbell et al., 1999; Ruiz et al., 2010). Under the assumption of neutrality, response to fire should not vary significantly among taxa. This would mean that whether a tree dies or not due to fire is a result of individual tree morphological variables, like girth and growth rate, in addition to the stochasticity of fire variables such as fire temperature at the foot of each tree, but not to its taxonomic identity (Barlow et al., 2003a,b; Romero and Bolker, 2008; Balch et al., 2011). In contrast, under non-neutrality, an individual's response would be taxon-specific. Such taxon-specific effects could be related to biological attributes that can determine differential species-specific responses to the disturbance, but also to the specific quality of the site for a given taxon ("niche")—allegedly manifested in species' relative abundance—or to species mortality rates under non-disturbed conditions (background mortality). Traits such as thickness of the bark and differential heat-insulating properties as well as greater resprouting or coppicing ability have been regarded as particularly relevant to species survival (Uhl and Kauffman, 1990; Cleary and Priadjati, 2005). In turn, these factors may vary among species according to their successional status (Slik, 2004; Slik et al., 2008), from pioneer species, to light gap heliophiles, to long-lived, mature forest canopy species.

In this study, we attempt to investigate the patterns of tree mortality in tropical forests after disturbances such as understory fires or after intense droughts. We aim at testing two non-exclusive hypotheses: (i) mortality after fire or drought has a species-specific basis related to taxonomic identity, and species ecological performance (i.e., successional status), and (ii) the likelihood of individual trees to die after such disturbances is on a stochastic basis, influenced by individual tree's features such as basal area/age and growth rate. These hypotheses are relevant to the application of neutral theories to explain the dynamics of tropical forests under disturbance regimes characterized by new agents, such as fire.

1.1. Study sites

The localities used for this study are within the Eastern lowland rain forest of the Southern Autonomous Atlantic Coast Region of Nicaragua. It is part of the Central American Eastern seaboard everwet lowland forest extending from southern Honduras to Southern Costa Rica. The forest receives 4320 mm of rain annually, with an 8–10 week dry season from early February to late April, a period where monthly precipitation drops to 75–125 mm (data from NOAA weather station in Bluefields). The sites were part of a long-term project that followed rain forest regeneration after Hurricane Joan, a category 4 hurricane that struck the Autonomous Southern Atlantic Region (RAAS) of Nicaragua in October of 1988. The trajectory of the eye of the hurricane very closely followed the 12° parallel, passing precisely over the city of Bluefields, the region's capital. Every year since the hurricane, our group has been monitoring several sites within lowland forest fragments along the Nicaraguan Caribbean coast affected by the hurricane (Boucher et al., 1990; Vandermeer et al., 1990; Yih et al., 1991). In the first decade after the hurricane, the forest had been regenerating at a

rapid pace (Boucher et al., 2001; Granzow-de la Cerda et al., 1997; Vandermeer et al., 2001; Ruiz et al., 2001; Vandermeer and Granzow-de la Cerda, 2004), but at the same time it had been progressively encroached by increased human activity that significantly modified the landscape. It is within the agricultural frontier prevalent in most of Eastern Nicaragua. During the first decade of our studies, in the 1990's, the landscape became a patchwork of forest fragments, land used for various types of agricultural purposes, and abandoned agricultural land. Other types of vegetation are also present in the region, such as fire-maintained savannas and swamp forests, the type of landscape that now prevails along the Eastern coast of Central America, from southern Honduras well into Costa Rica.

Our data contains an 18-year continual record of forest succession from 1990 to 2007. All adult trees and large saplings (>3.18 cm dbh, i.e. >10 cm circumference) in the study sites have been identified, tagged, mapped, and their dbh measured yearly. Between 1996 and 2006, measurements of tree height were also taken. The same procedure was followed for newly recruited individuals. The complete history of these sites and the methods for collecting data can be found elsewhere (Granzow-de la Cerda et al., 1997; Mascaro et al., 2005; Vandermeer et al., 2001). Our post-ENSO fire study used the four permanent sites established in successive years following the landfall of Hurricane Joan in 1988. They are included within a band between 14 km south and 30 km north of Bluefields—on each side of the trajectory of the hurricane's eye—all within the same lowland rain forest matrix that was strongly affected by the hurricane, with the two farthest apart being less than 50 km from each other. Two of the sites, set up shortly after the hurricane (1989 and 1990) at sites named Bodega and Fonseca, consist of three 10 × 100 m transects each. Two additional sites, geographically located between the first two, were set up in 1994 in the sites known as Loma de Mico and La Unión, respectively, each consisting of a single 30 × 50 m plot. In successive years after 1999, two 30 × 50 m were added in Bodega and two in La Unión, which facilitated determination of background mortality (in the absence of fire or drought). The total area for all plots and transects add up to 1.5 ha, which collectively includes 4100 trees and large saplings, representing at least 255 taxa.

The fires that swept through vast extensions of the Central American landscape occurred toward the end of the prolonged dry season brought about by the 1998 ENSO event. The plots and transects in this study burned at least 1 month after our yearly field data-collecting campaign of February–March. The fires behaved as “understory” or “ground” fires (Lloret and Zedler, 2009; van Nieuwstadt, 2002) that mostly burned accumulated leaf litter, producing low flames and dense smoke. Intensity of the fire (in terms of heat) was relatively mild, to the extent that narrow natural firebreaks, such as a 2 m-wide active trail, would act as a fire-break. When the fires occurred, 10 years after the hurricane struck, the forest had an upper diffuse canopy that reached 25–30 m in height over a lower, very dense canopy of ca. 10 m (the “thinning canopy”, as described in Vandermeer and Granzow-de la Cerda, 2004).

Three of our four sites were subject to fires. In Fonseca, two transects burned, as did the sole plot in Loma de Mico, while in Bodega only one of the three initial transects burned. Fires never spread into the single plot at La Unión. The existence of well-travelled forest paths, even if narrow, in Bodega and the swift action of farmers cutting firebreaks as fires advanced in La Unión, prevented those transects and plots from burning. Data on mortality were collected during the following field season, February to March 1999, for all plots and transects—burned and unburned. Data were collected again the following season, in 2000, from the same transects and plots to determine delayed mortality. No biotic or abiotic indicator could be determined for ranking fires by their intensity.

We found evidence that in burnt plots significant heat was produced just within the 30–50 cm closest to the ground. The lowermost 20–30 cm of PVC tubes used for marking plots and transect were consistently found melted at their base in burnt sites. Nine to ten months after the fires, no signs of charred trunks above that height were found and only occasional charred branches were seen on the ground. Occasionally some trees showed a charred bark, usually below the lowermost 30 cm, or between buttresses, arguably where accumulation of dry leaf litter is greatest. No further evidence of fire damage was observed. After the fires, leaf litter cover seemed to be thinner than usual (no data were collected to this effect) although presence of charred leaf remnants or ashes were not expected after 10–11 months of weathering.

2. Methods

The 15 most abundant species in the 1999 census were used to analyze differences in mortality among taxa. They had to be represented in the three sites that burned and in the two sites that did not burn, with at least 10 individuals among the burned sites and 10 among the unburned ones. However, species missing from just one site (either burned or unburned) were included if they had at least 15 individuals in total in the remaining sites (burned or unburned; marked with † in Table 1).

A larger set of species was used to run analyses comparing ecological guilds (Table 1). These taxa in the 1999 census were represented by at least eight individuals in total (dead or alive) occurring in two or more sites that burned and at least one individual (dead or alive) in a site that did not burn. Taxa present in just one burnt site were accepted if they were represented by at least 25 individuals in the other burnt sites. An exception was made with the very common pioneer *Cecropia obtusifolia*, which was included in the analyses despite having only five individuals between two burnt sites (all dead in 1999) but 23 in the two unburned sites. The most abundant taxon overall, the palm *Astrocaryum alatum* H.F. Loomis, was excluded from the study because measurements of basal area were excessively inaccurate or missing for many individuals. This brought the total tree count in burnt and unburned plots and transects to 1863 trees belonging to 38 species, which collectively constituted 49% and 45% of the pre-fire total basal area for all burnt and unburned plots, respectively (Table 1). Taxa were assigned to one of five guilds according to their successional stage or ecological characteristics (“niche”): (1) pioneers; (2) subcanopy/understory heliophiles; (3) canopy heliophiles; (4) subcanopy mature forest species; (5) canopy mature forest species (Table 1, modified from Vandermeer and Granzow-de la Cerda, 2004). The two species considered here as pioneers can be well characterized as such based on fast growth, colonizing disturbed places, low wood density and small seed size. The remaining taxa were assigned to heliophile guilds (2 and 3) if present in existing plots set in nearby abandoned pastures and early successional forest tracts at the La Unión site. For species that were absent from plots in any type of vegetation at La Unión site, the criteria for guild allocation were based on species descriptions from regional floras (Flora de Nicaragua and Flora Mesoamericana, Stevens et al., 2001; Davidse et al., 1997, respectively, online versions). Assignment to either the understory/subcanopy guilds (2 and 4) or to the canopy guilds (3 and 5) was based on species' average tree volume (basal area × height). Species were ranked by the fourth quartile of tree volume, with the cutting point between understory/subcanopy and canopy guilds set at the greatest discontinuity between taxa (such that average tree volume of the smallest canopy species, *Byrsonima crassifolia* of guild 3, was 61% greater than that of the largest subcanopy/understory species, *Pera arborea* of guild 4).

Table 1

Number of individuals belonging to the 38 most abundant species present in plots and transects that burned during the 1998 fires. Trees are segregated on whether their plot/transect was affected by fire or not. The species are grouped into five ecological guilds, defined as: (1) pioneers; (2) subcanopy/understory heliophiles; (3) canopy heliophiles; (4) subcanopy mature forests species; (5) canopy mature forest species. Basal area values are from the census of, 1998, taken a few weeks before the fires. In bold and marked with † are the 15 most abundant species, used for the analysis at the individual species level.

Taxon	Family	Nr. trees alive Prior to fires (1998)		Surviving trees 1998–1999						Surviving trees 1999–2000		
		Un-burned plots	Burnt plots	Un-burned plots		Burnt plots		Expected survival burnt 1998 to 1999	% of 1998 basal area in		% survival	
				Nr. of trees	% Surv.	Nr. of trees	% Surv.		Un-burned plots	Burnt plots	Un-burned plots	Burnt plots
<i>Cecropia obtusifolia</i> Bertol.	Urtic.	23	5	17	74	0	0	13.5	0.84	0	88	–
† Croton smithianus Croiz.	Euphorb.	44	40	30	68	13	33	23.8	0.87	0.43	93	64
(1) Pioneer (guild)	Total	67	45	47	70	13	29	37.3	0.86	0.4	91	64
† Guatteria recurvisepala	Annon.	40	59	31	78	18	31	24.6	0.79	0.43	100	94
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<i>Hirtella americana</i> L.	Chrysobal.	10	25	10	100	18	72	7.9	1	0.9	100	100
† Isertia haenkeana DC.	Rub.	12	28	9	75	10	36	7.1	0.6	0.43	89	70
<i>Lacistema aggregatum</i> (Berg) Rusby	Lacistemat.	39	9	38	97	4	44	30.1	0.99	0.42	100	75
† Miconia prasina (Sw.) DC.	Melastom.	59	153	58	98	82	54	46	0.97	0.58	97	77
(2) Subcanopy/understory heliophiles (guild)	Total	160	274	146	91	132	48	115.8	0.9	0.66	98	81
† Byrsonima crassifolia (L.) Kunth	Malpigh.	21	23	21	100	18	78	16.7	1	0.77	100	93
† Dendropanax arboreus (L.) Dec. & Planch.	Aral.	99	17	91	92	9	53	72.2	0.96	0.61	99	88
<i>Inga thibaudiana</i> DC.	Mimos.	13	8	13	100	3	38	10.3	1	0.47	92	100
† Simarouba amara Aubl.	Simaroub.	14	13	14	100	6	46	11.1	1	0.77	100	100
† Vochysia ferruginea Mart.	Vochys.	88	102	86	98	46	45	68.2	1	0.64	98	89
<i>Xylopia frutescens</i> Aubl.	Annon.	11	13	11	100	11	85	8.7	1	0.84	100	100
(3) Canopy heliophiles (guild)	Total	246	176	236	96	93	53	187.1	0.98	0.66	98	92
<i>Amaioua corymbosa</i> Kunth	Rub.	11	32	11	100	24	75	8.7	1	0.9	100	77
<i>Angostura granulosa</i> (Kallunki) Kallunki	Rut.	2	33	2	100	18	55	1.6	1	0.56	100	89
<i>Ardisia</i> sp.	Primul.	2	21	2	100	13	62	1.6	1	0.69	50	82
<i>Croton schiedeana</i> Schlecht.	Euphorb.	4	15	4	100	5	33	3.2	1	0.3	100	80
† Cupania glabra Sw.	Sapind.	49	118	49	100	48	41	38.9	1	0.38	100	69
<i>Miconia elata</i> (Sw.) DC.	Melastom.	8	14	8	100	4	29	6.3	1	0.26	100	33
<i>Miconia punctata</i> (Desr.) D. Don ex DC.	Melastom.	3	9	3	100	4	44	2.4	1	0.46	100	33
<i>Pera arborea</i> Mutis	Euphorb.	1	8	1	100	6	75	0.8	1	0.78	100	80
<i>Prestoea decurrens</i> (Burret) H.E. Moore	Arec.	4	15	3	75	10	67	2.4	0.91	0.67	100	78
† Protium confusum (Rose) Pittier	Burser.	32	22	32	100	6	27	25.4	1	0.46	97	100
<i>Psychotria panamensis</i> Standl.	Rub.	7	8	6	86	3	38	4.8	0.67	0.3	100	33
† Rinorea squamata Blake	Viol.	30	60	29	97	31	52	23	0.95	0.6	93	61
<i>Unonopsis pittieri</i> Saff.	Annon.	7	9	4	57	5	56	3.2	0.17	0.76	100	0
(4) Subcanopy mature forest species (guild)	Total	160	364	154	96	177	49	122.1	0.88	0.56	97	72
<i>Carapa guianensis</i> Aubl.	Mel.	2	12	2	100	4	33	1.6	1	0.29	100	100
† Cordia bicolor A. DC.	Boragin.	13	10	12	92	8	80	9.5	0.85	0.82	92	63
<i>Hirtella guatemalensis</i> Standl.	Chrysobal.	2	26	2	100	14	54	1.6	1	0.78	100	64
† Inga cocleensis Pitt.	Mimos.	18	40	17	94	23	58	13.5	0.91	0.78	100	65
† Mabea occidentalis Benth.	Euphorbi.	15	23	15	100	11	48	11.9	1	0.57	100	75
<i>Manilkara zapota</i> (L.) Royen	Sapot.	5	21	5	100	17	81	4	1	0.96	100	75
† Pseudolmedia spuria (Sw.) Griseb.	Mor.	22	32	22	100	18	56	17.4	1	0.84	95	87
<i>Qualea lineata</i> Stafleu	Vochys.	18	25	18	100	23	92	14.3	1	0.97	100	--
<i>Spaichea correae</i> Cuatr. & Croat	Malpigh.	3	13	3	100	7	54	2.4	1	0.93	100	86
<i>Terminalia amazonia</i> (J.F. Gmel.) Exell	Combret.	17	9	17	100	6	67	13.5	1	0.89	100	80
<i>Tetragastris panamensis</i> (Engl.) Kuntze	Burser.	6	23	6	100	12	52	4.8	1	0.72	100	83
<i>Virola multiflora</i> (Standl.) A.C. Sm.	Myristic.	8	8	8	100	5	63	6.3	1	0.89	100	67

(continued on next page)

Table 1 (continued)

Taxon	Family	Nr. trees alive Prior to fires (1998)		Surviving trees 1998–1999						Surviving trees 1999–2000		
		Un-burned plots	Burnt plots	Un-burned plots		Burnt plots		Expected survival burnt 1998 to 1999	% of 1998 basal area in		Un-burned plots	Burnt plots
				Nr. of trees	% Surv.	Nr. of trees	% Surv.		Un-burned plots	Burnt plots		
(5) Canopy mature forest species (guild)	Total	129	242	127	98	148	61	100.7	0.98	0.85	98	78
Total all guilds	1863	762	1101	710	93	563	51		0.95	0.7	98	78

Throughout this paper, we consider surviving individuals those that remained alive in any given year from a previous one. Therefore, survival for a species in 1999 was the number of live individuals in 1998 that survived to 1999. Background survival is the probability of survival from one year to the next in the absence of fire in non-ENSO years.

For tree size, we used basal area (log transformed) from the previous year's census. Thus, when survival in 1999 was related to size, the basal area data used was that of 1998, and so on for every year. Similarly, annual growth rate was defined as the median of year-to-year change in circumference at breast height for the 5 years prior to the year of concern (but not including size or growth from the current year); e.g., to correlate relative growth rate with survival in 1999, the median of year-to-year growth for 1993–1994, 1994–1995, 1995–1996, 1996–1997 and 1997–1998 was used.

Analyses were carried out under two scenarios: (1) effect of fire and (2) effect of drought. Within each scenario, two criteria were considered: (1) Taxonomic identity (each one of the 15 most abundant species individually), and (2) species grouped by their successional status (the 38 most abundant taxa grouped into five guilds). To determine whether there was differential survival based on taxonomic identity among those 15 most abundant species, we conducted a Breslow-Day test for homogeneity, comparing survival pre-fire and pre-drought, to survival under the post-fire and drought scenarios.

To assess the effect of fire and drought on survival we carried out two separate analyses, one for each of the scenarios (post-fire and drought effect) by means of multiple logistic regression using the JMP package for MacOSX (www.jmpdiscovery.com, SAS Institute, ver. 5.0).

The first set of regression models was aimed at determining the effect of fire on survival. Tree survival within the first year after the fires (from 1998 to 1999) was used as the response variable. An additional iteration of the model was carried out to examine survival in the second year following the fires for the sites with burnt plots. Here, survival of trees from the first to the second year after fires (1999–2000) was used as the response variable.

The second model assessed the effect of ENSO-related drought on survival for plots that did not burn. To assess differences in survival as a result of ENSO drought, data from the 1999 census were compared to data from censuses from all other years and all other plots, i.e., comparing survival on a dry year to “background” survival of non-ENSO years. To do this, obviously, only plots that did not burn in 1998 (but were subject to drought) were compared against drought-free years. Data from the 2000 census were purposely excluded as trees may have lasting effects 2 years after the drought and cannot qualify as drought-free. Data from plots established after the ENSO year were also used to establish background conditions. Survival for a specific year was used as the response variable.

The independent variables for both models were: (1) Occurrence of fire (burnt/not-burned) in a plot; (2) guild; (3) tree basal area (log N) in 1998; and (4) relative growth rate in dbh (the latter used only in the model for the effect of fire). Results for these variables and their interactions are presented in Tables 2 and 3.

3. Results

3.1. Effect of fire on survival

Out of the total 1863 individual trees alive in the February/March 1998 census, 762 were in plots not affected by the 1998 ENSO fires, and 1101 were in plots that burned. During the 1999 census, 710 trees (93%) were still alive in unburned plots and transects, while in burned plots mortality was higher, with only 563 (51%) trees remaining alive (Table 1). A delayed mortality effect was observed in the plot in Loma de Mico and two transects in Fonseca that were monitored again in 2000. Of the 710 trees alive in 1999 in unburned plots and transects, 693 (98%) survived to 2000, while in the burned plot and transects that were studied a second year, out of 455 trees alive in 1999, only 355 (78%) survived to 2000. For both, 1999 and 2000, survival in burned plots and transects was significantly lower than in those that did not burn.

3.1.1. Taxonomic identity criterion

Response to fire among individuals from the 15 most abundant taxa was heterogeneous in unadjusted analyses, and the mortality experience across species during fire differs from mortality experience across species in absence of fire (Breslow-Day test for homogeneity $\chi^2 = 34.37$, d.f. = 14 $p = 0.0018$). However, in the multiple regression the taxon \times burn/no-burn interaction was not significant (Table 2).

3.1.2. Guild criterion

The grouping of the 38 species into five guilds (see Table 1) showed that overall tree survival in burned plots between 1998 and 1999 was significantly lower ($p < 0.0001$) than in unburned plots for all guilds. The canopy mature forest species guild (guild 5) had the highest survival rate (98% in unburned plots, 61% in burnt ones). Overall differences in survival among guilds were significant, but only because of the disproportionately low survival rate of the pioneer guild (guild 1) after fire ($p < 0.0001$, Table 2). In unburned plots pioneers survival was 70%, significantly lower than other guilds ($p < 0.0001$ to $p = 0.0088$, Fig. 1A). With survival as low as 29% in burnt plots, pioneers differed significantly from the canopy mature species guild ($\beta = -0.278$, $p = 0.01$) and, to a lesser extent, from guilds 3 and 4 ($\beta = -0.272$, $p = 0.018$, and $\beta = -0.224$, $p = 0.036$, respectively). However, survival rates for the other three guilds: understory heliophiles, canopy heliophiles and understory mature forests species (48%, 53% and 49%, respec-

Table 2

Results from multiple logistic model for the effect of fires on survival for 38 tree species, corresponding to 1999 and 2000, 1 year and 2 years after the 1998 ENSO fires, respectively. Guilds are defined as: (1) pioneers; (2) subcanopy/understory heliophiles; (3) canopy heliophiles; (4) subcanopy mature forests species.

Source	d.f.	Chi square	Prob > ChiSq	d.f.	Chi square	Prob > ChiSq
Taxon (15 spcs., random)	14	43.626	0.0001			
Burnt/not-Burned	1	0.338	0.5611			
Taxon * B/N (random)	14	13.273	0.5052			
Burnt/not-Burned	1	174.71	<0.0001	1	53.33	<0.0001
Guild	4	56.645	<0.0001	4	4.635	0.327
Burnt/not-Burned * Guild	4	8.938	0.0627	4	2.275	0.685
LnBasAr 98	1	26.368	<0.0001	1	3.163	0.075
B/N * 98 LnBasAr	1	11.800	0.0006	1	0.000	0.994
Guild * 98 LnBasAr	4	16.621	0.0023	4	2.603	0.626
Relative growth 93–98	1	2.244	0.1341	1	1.903	0.168
Burnt/Not-B * Rel. growth 93–98	1	11.632	0.0006	1	2.335	0.127
Guild * Rel. growth 93–98	4	12.071	0.0168	4	6.635	0.157

Table 3

Results from logistic models for the effect of drought (following the ENSO event, 1999) on survival for 38 tree species against background survival (non-ENSO years, 1990–1998 and 2000–2007) for plots that did not burn in the 1998 fires. Guilds are defined as: (1) pioneers; (2) subcanopy/understory heliophiles; (3) canopy heliophiles; (4) subcanopy mature forests species.

Source	D.F.	Chi Square	Prob > ChiSq
Taxon (15 spcs., random)	14	87.049	<0.0001
Drought (ENSO/non-ENSO year)	1	0.119	0.730
Taxon * drought (random)	14	10.661	0.712
Drought (ENSO/non-ENSO year)	1	4.146	0.0417
Guild	4	138.22	<0.0001
Drought * guild	4	5.277	0.26
LN BasArea (previous year)	1	24.102	<0.0001
Drought * LN BasArea	1	0.154	0.6948

tively, in plots that burned, 91%, 96% and 96%, respectively, in plots not burned) did not differ significantly between each other under fire or non-fire conditions (Table 2, Fig. 1A).

In burned plots that were surveyed a second year, in 2000, all guilds except for canopy heliophiles showed a delayed mortality

effect, as survival rates from 1999 to 2000 were significantly lower in plots that burned compared to plots that never burned ($p < 0.0001$). Pioneers remained the guild with lowest survival in burnt plots (*Croton smithianus* had 64% survival from 1999 to 2000, while *C. obtusifolia* had surviving individuals in 1999), but only differed significantly from the guild with the highest survival—canopy heliophiles: $\beta = -0.361$, $p = 0.01$). Heliophiles (guilds 2 and 3)—especially canopyheliophiles—on the other hand, had the highest survival rate in burnt plots (81% and 92%, respectively; Fig. 1B), while mature forest species (guilds 4 and 5) had the lowest mortality in those same plots (72% and 78%, respectively) and their survival was significantly lower than in plots that were not burnt ($\beta = -0.332$, $p < 0.0001$ for guild 4, $\beta = -0.239$, $p = 0.0005$ for guild 5). Thus, the effect of delayed post-fire mortality among guilds was significant when comparing survival of guilds 4 and 5 with that of guild 3, the one with highest survival ($\beta = -0.313$, $p = 0.0001$ and $\beta = -0.194$, $p = 0.014$, respectively). No significant differences between guilds existed in plots that did not burn.

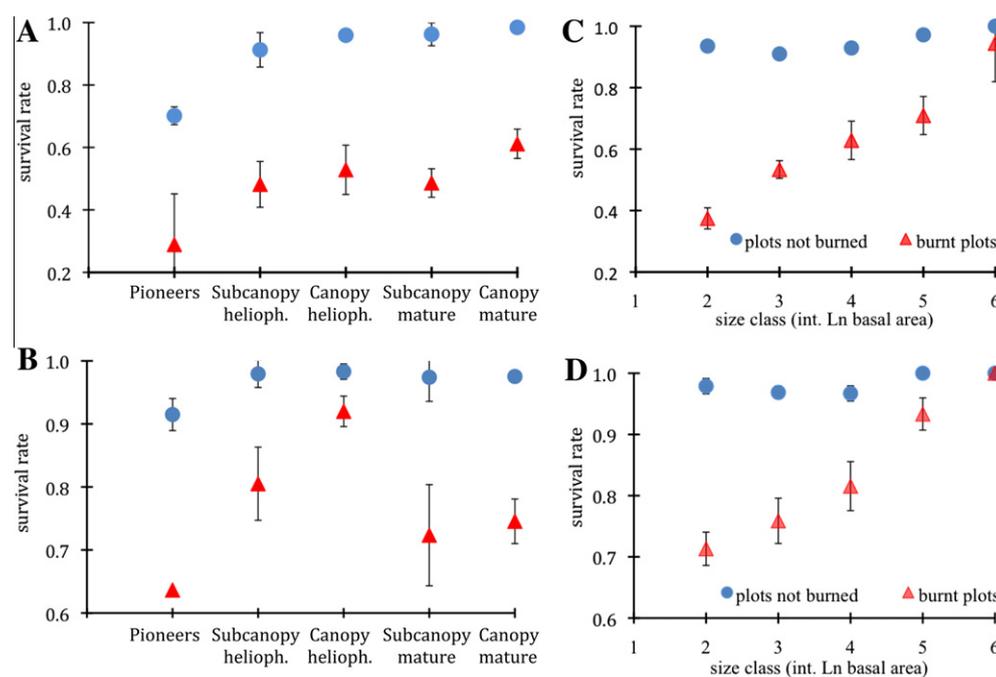


Fig. 1. Effect of fires on survival for the 38 most abundant species in plots and transects that burned (triangles) and in those not affected by fires (circles). (A) Average survival rate for species grouped by guild the year following the fires (from 1998 to 1999). (B) Average survival rate for species grouped by guild, 2 years after the fires (from 1999 to 2000). (C) Average survival rate for individuals grouped by size classes, the year following the fires (from 1998 to 1999). (D) Average survival rate for individuals grouped by size classes 2 years after the fires (from 1999 to 2000). Size classes correspond to integer of log *N* of tree basal area, measured prior to the fires. 2: 3.10 to 5.06; 3: 5.07 to 8.34; 4: 8.35 to 13.75; 5: 13.76 to 22.66; 6: 22.67 to 37.37; 7: >37.38.

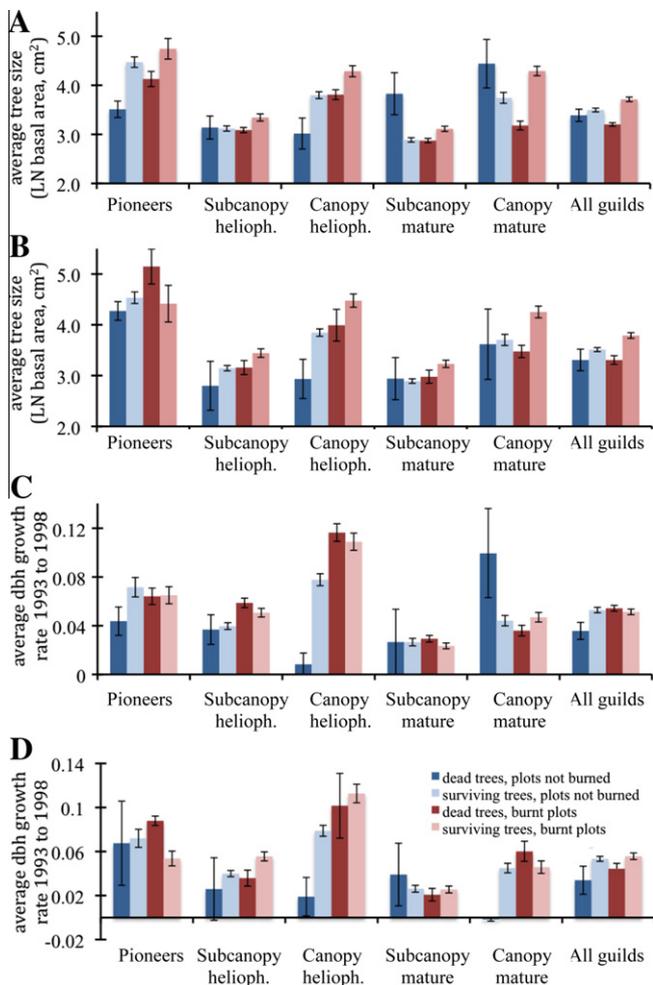


Fig. 2. Average tree size (LN basal area measured prior to the fires) and average relative growth rate in dbh (median of yearly growth from 1993 to 1998) of dead and surviving trees in plots and transects that did not burn, and those that burned. Individual trees are grouped by guild, and values are given for all plots combined. (A) Average tree size the year following the fires (1999 census). (B) Average tree size the second year after the fires (survival from 1999 to 2000). (C) Relative growth rate of trees the year following the fires (1999 census). (D) Relative growth rate of trees the second year after the fires (survival from 1999 to 2000).

3.1.2.1. Tree size and growth rate effects. We found a strongly significant overall positive effect of tree size (log *N* of basal area as measured prior to the fires) on survival ($p < 0.0001$). Survival is positively correlated with size under fire conditions, and significant differences exist between non-contiguous size classes (Fig. 1C). The burnt/not burned \times tree size interaction was significant ($p = 0.0006$, Table 2) due to the strong positive effect of size in burnt plots, overall and for all guilds (Fig. 2A), especially among pioneers and canopy guilds (1, 3 and 5). However, in unburned plots the effect of size on survival was not significant overall, and even had a significant negative effect in mature forest guilds (4 and 5, Fig. 2A). Relative growth rate (median yearly growth for at least 3 years prior to the fires) had no significant overall effect on survival, at least in burnt plots, but the interaction with burnt/not burned condition was significant and positive ($p = 0.0006$, Table 2). In unburned plots, faster growth was associated with higher odds of survival only among pioneers and canopy heliophiles, but non-significant in the rest, and even negatively so in canopy mature forest species (Fig. 2C).

For trees measured in 2000, basal area had a marginally significant positive effect in improving survival overall ($p = 0.012$; Table 2, Fig. 1D), but no interaction was observed by burnt/

unburned conditions. Size had little effect on delayed mortality on a guild-by-guild basis, as by the second year after fires no significant size difference between dead and surviving trees was observed for any guild other than the canopy mature forest species (Fig. 2B). Growth rate in dbh had little overall effect on second year survival, regardless of fire status (Table 2). The only guild where faster growing trees showed better survival 2 years after fire were the subcanopy heliophiles, while pioneer trees with faster growth remained significantly affected by delayed mortality (Fig. 2D).

3.2. Effect of drought on survival

During the 1998–1999 season all trees in all plots were subjected to the uncommon drought caused by that year's ENSO. When considering only plots that did not burn (the sites of Bodega and La Unión had such plots), survival between 1998 and 1999—the year of the drought—was significantly lower, overall, than background survival (in the preceding and following years: 1992–1998 and 2000–2007, respectively: $p = 0.042$, Table 3).

3.2.1. Taxonomic identity criterion

Mortality experience across species during drought differs from the mortality experience during non-drought years (Breslow-Day test for homogeneity, $\chi^2 = 97.02$, d.f. = 14, $p < 0.0001$) showing also great heterogeneity among individuals in their response to drought.

3.2.2. Guild criterion

Only the pioneers were found to have significantly worse survival the year of ENSO as compared to the non-ENSO years ($p < 0.0001$). Overall, differences in survival among guilds were significant ($p < 0.0001$, Table 3), as a result of the high mortality of pioneers the year of the drought. During the ENSO year, survival of pioneers was even lower when compared to all guilds (differences with guilds 2, 3, 4, and 5, $\beta = -0.25 \pm 0.04$, respectively, $p < 0.0001$), while survival differences between all other guilds were non-significant (Fig. 3A). Therefore, the different behavior of pioneers was not enough to produce a significant guild \times drought interaction (Table 3) in the adjusted analyses.

3.2.2.1. Tree size effect. In the model, tree size (LN of basal area) shows an overall significant positive effect on survival across all years (ENSO and non-ENSO, $p = 0.0001$, Table 3) with no significant interaction between size and drought (Table 3). Survival is positively correlated with size for the ENSO year, and significant differences exist between non-contiguous size classes (Fig. 3B). Overall, individuals that survived during the ENSO year were significantly larger than the ones that died. This was particularly true for pioneers and canopy mature forest species (guilds 1 and 5), while no size effect on survival was observed among heliophiles and subcanopy mature species (guilds 2, 3 and 4; Fig. 3C).

4. Discussion

4.1. The effect of fires

Within a year of their occurrence, surface forest fires caused dramatic mortality among trees in tropical rain forests. However, the ENSO-driven drought that facilitated the fires compounded the effect of fire on overall mortality. An additional number of trees died 2 years after fires (between 1999 and 2000), and post-fire resprouts were almost invariably dead, a finding that agrees with the delayed mortality effect reported for resprouting species in other types of ecosystems, including those from Mediterranean regions (Lloret and López-Soria, 1993). The community assemblage shifted

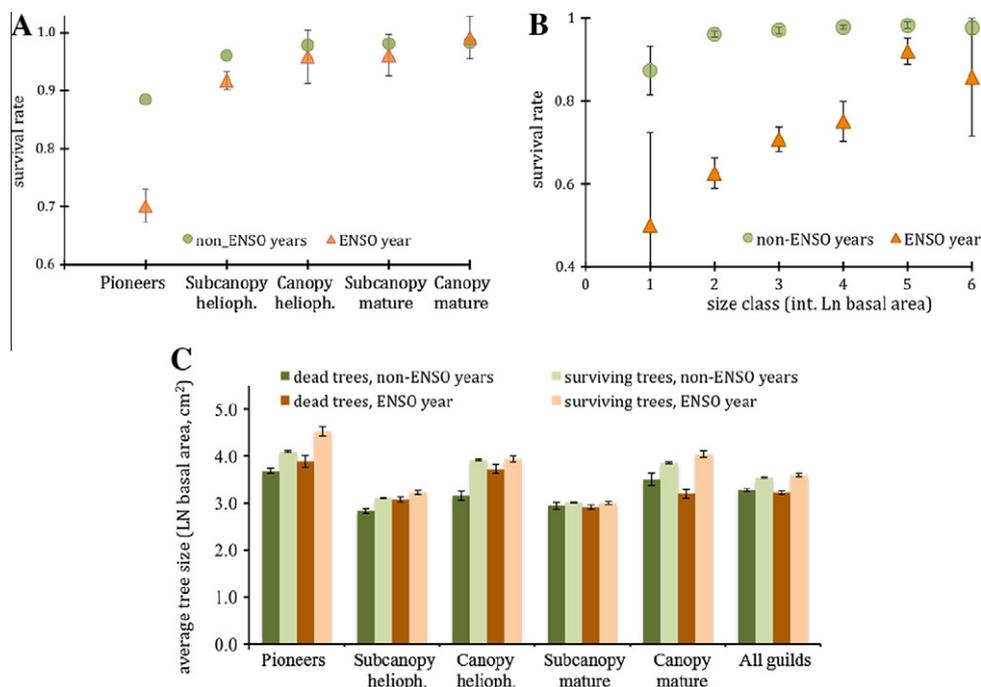


Fig. 3. Effect of 1998 ENSO drought on survival of the 38 most abundant species in plots and transects during the 1998–1999 ENSO year drought, and in those in non-ENSO years, 1991–1998 and 1999–2007, not subjected to drought. Only plots that did not burn in 1998 were included in the analysis. (A) Average survival rate for species grouped by guild for ENSO year (triangles) and non-ENSO years (circles). (B) Average survival rate for individuals grouped by size classes, for ENSO year (triangles) and non-ENSO years (circles); size classes correspond to integer of log N of tree basal area, measured prior to the fires. 2: 3.10 to 5.06; 3: 5.07 to 8.34; 4: 8.35 to 13.75; 5: 13.76 to 22.66; 6: 22.67 to 37.37; 7: >37.38. (C) Average tree size of dead and surviving trees, grouped by guild, and for all guilds combined, in plots and transects for ENSO and non-ENSO years.

toward greater presence of heliophilous herbs and vines as the canopy became increasingly open.

Heterogeneity among individual taxa in their response to fire is large. Differences in survival between the 15 most abundant species after fire suggest species-specific responses. We have not attempted to find correlations between mortality rates after fires and taxon-specific differences in morphological traits, although a number of traits such as bark thickness have been regarded in some studies as responsible for differential survival among species (van Nieuwstadt, 2002; Baker et al., 2008; Slik et al., 2010; Fensham et al., 2003 for northern Australia; Barlow et al., 2003a,b for central Amazonia).

Grouping taxa into guilds according to their ecological or successional status provides more robust results that show significant differences in survival among guilds ($p < 0.0001$). To infer the successional status of taxa, we relied on our species assemblage data on presence or absence from mature and/or secondary forest tracts in the area, as well as tree height. Compared to the other guilds, pioneers were found to be more vulnerable to fire (Fig. 1A and B), with only 33% survival in *C. smithianus* and no survival in *C. obtusifolia* (Table 1). *C. smithianus* had been rather common in the forest canopy since the hurricane, with numerous large individuals whose abundance declined during the 10 years that lapsed between the hurricane and the ENSO fires, suggesting age-dependent mortality of cohorts due to competitive interactions when the canopy closed up. However, the low survival of pioneers, *C. smithianus* and *C. obtusifolia*, in both scenarios, with and without drought (70% during ENSO, ca. 89% as background survival–non-ENSO years) is the main source of difference in overall survival among guilds (Fig. 1A).

Fire-related mortality of trees in these forests showed that in addition to individual traits such as tree size or relative growth (Fig. 2), there is a stochastic component to tree survival, so for most species, taxonomic identity *per se* has little effect on survival. Surviving trees in burnt plots were significantly larger than dead ones

across guilds, but in unburned plots, surviving trees were significantly larger than dead ones only among pioneers and canopy heliophiles. In the pioneer guild, where overall survival was comparatively low, the positive effect of size on survival was significant in burnt as well in unburned plots. The observation that in some cases, such as mature forest guilds, smaller trees are more vulnerable to fire is consistent with results reported elsewhere, for example, from Borneo after the same 1998 ENSO event (Slik and Eichhorn, 2003; Slik, 2004; van Nieuwstadt and Sheil, 2005; Slik et al., 2008) or for burn experiments in the Brazilian Amazon (Balch et al., 2011), or others (Barlow et al., 2003a,b). Allegedly, larger trees, with a thicker bark that provides better protection, are more likely to cope with heat (Pinard et al., 1999; Eriksson et al., 2003). In plots that did not burn, surviving trees of mature forest species guilds (4 and 5) were significantly smaller than the ones that died (Fig. 2A). This finding suggests a greater susceptibility to drought among large trees from mature forest species. One needs to consider that in that year of ENSO (1998–1999), plots that did not burn were still subject to an exceptionally long drought.

The patterns above are carried over to the following year (2000): surviving trees are significantly larger than the ones that died 2 years after the fires (Fig. 1C). All guilds, presented this behavior. Although non-significant for most guilds, surviving trees in unburned plots tend to be larger than those that die. In burnt plots, trees that survived by the second year were significantly larger than the ones that did not only among the mature forest guilds (4 and 5), while the pioneers showed a trend in the opposite direction: trees that suffered delayed mortality after 2 years tended to be larger than the survivors (Fig. 2B).

Despite the significant association between relative growth and background survival rate in the absence of fire (trees that grow faster and reach the canopy are more likely to survive, as shown in Vandermeer et al., 2001; Vandermeer and Granzow-de la Cerda, 2004), this positive association between growth rate and survival is not obvious under fire conditions (Fig. 2C). Rather, the opposite

is true for the mature species guild without fires. In unburned plots, dead canopy mature forest species had been growing faster than surviving ones. This result may reflect increased vulnerability to drought in fast growing trees from mature forest guilds subjected to that year's drought conditions. This finding stresses the negative effect that drought has had on fast growing mature forest canopy trees.

4.2. The effect of drought

The drought associated with the 1998 ENSO episode may have reduced overall tree survival, regardless of occurrence of fire. In fact, a significant species-specific differential in survival exists in relation to drought. Survival in unburned plots was significantly reduced the year after the 1998 ENSO event when compared with non-ENSO years. This observation is consistent with other findings of drought-induced mortality in tropical forests (for instance, Newbery and Lingenfelder, 2004, in Sabah, Borneo). However, mortality rates induced by drought were not as high in our system as those reported from other regions during that same ENSO event (van Nieuwstadt and Sheil, 2005 in East Kalimantan). The pioneer guild, again, shows greater mortality than any other guild, certainly for the ENSO year, but pioneers also had the highest background mortality (during non-ENSO years, Fig. 3A). The significant overall decline in survival due to drought at a guild level (Table 3) is mostly driven by the high mortality of the pioneer guild, as there are no significant differences in mortality among the rest of guilds, with or without drought (Fig. 3A). As expected, most forms of disturbance accentuate the already predictable short lifespan of pioneers, but for most other guilds, whether heliophiles or mature forest species, droughts of this intensity have very limited effect in reducing survival, as long as fires do not occur.

The effect of tree size on survival is quite different when uncoupled from species and guild effects. While no significant differences in survival existed between size classes under no-drought conditions, there was a positive correlation between size and survival the year of the drought (in spite of a trend toward diminished survival by the largest size class, Fig. 3B). Similarly to what happened in response to fires, the strong overall size effect on survival (regardless of taxon or guild) under drought is supported by the fact that size classes—at least non-contiguous ones—show significant differences in survival among each other. Evidence on the effect of drought from other studies (Slik, 2004; Slik et al., 2010; Balch et al., 2011) agrees with our results. Others, on the other hand, have found the opposite, pointing toward a greater vulnerability of large tropical rainforest trees that underwent ENSO droughts, particularly in SE Asia (Slik and Eichhorn, 2003; van Nieuwstadt and Sheil, 2005; Phillips et al., 2009, 2010). The latter suggests that the higher net demand for water in trees closest to the canopy—thus carrying out photosynthesis more actively—would result in additional stress for those individuals. Historically, one may assume, these forests have been exposed to recurrent drought disturbances that, nonetheless, allow them to recover rapidly. Fire, on the other hand, may be a newcomer to the dynamics of this system, forcing, at least in the short-term, irreversible changes in the plant community.

When grouping species by guild, the average size for trees in our forest that died during the drought was smaller than for those that survived. These size differences were significant for pioneers and canopy guilds, as well as when all guilds were pooled together.

There is a positive tree size effect for some guilds, such that survival after fire is significantly lower among small trees. This agrees with what has been observed elsewhere as the typical scenario for pioneers (Vandermeer et al., 1996) and coincides with the pattern of damage caused by the hurricane. While growth in girth may im-

prove survival in the absence of fire for some (but not all) guilds, it has no significant effect on survival for any guild after a burn.

With drought as a disturbance, the scenario changes, as for some guilds large trees seem to be at a disadvantage in dry years. In the absence of fire, but under intense drought conditions, growth rate has shown a negative effect on survival on canopy species from the more mature successional stages. Survival, whether background or affected by a disturbance in the form of fire or drought, varies significantly across a number of factors. Taxonomic identity and successional stage are certainly important, but these characteristics can be confounded by other variables such as individual basal area or relative growth in bole diameter, both of which seem to play some role in determining survival.

As a disturbance, fire could have in part a stochastic effect on the tree community. There has been no evidence of regeneration of our original tree community, at least not in the 8–10 years since the fires, with forest canopies remaining very open and an understory dominated by invasive vines and herbs, mainly Cyperaceae and Poaceae, similar to what has been reported elsewhere (Uhl and Kauffman, 1990; Cochrane, 2003). Compared to forest fires, hurricanes are a more frequent disturbance in Central America's rain forests. They may occur in the order of one every 100 years (Boucher, 1992), while fires this widespread are probably much more rare—although no data is available for the region. There is evidence that large storms maintain—if not enhance—diversity in these forests (Vandermeer, 1996; Vandermeer et al., 1990, 1996). However, contrary to hurricanes, where understory community grows back quickly and a dense tree canopy of lesser height is promptly re-established, regeneration after fires is far from maintaining the pre-disturbance species composition. Differences in the regeneration dynamics of the forest after even these low-intensity fires, versus the most destructive storms are non-trivial. They probably result from suppression of resprouts, coppices or epicormic branches caused by heat near the tree base, even if fire temperatures are relatively low. This would impede the kind of direct regeneration was seen after the category 4 hurricane that struck this same forest 10 years prior, making fires neither conducive to maintaining species assemblages nor species richness in these lowland rain forests.

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