

Effects of single and recurrent wildfires on fruit production and large vertebrate abundance in a central Amazonian forest

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Abstract. Wildfires are an increasing threat to tropical rainforests, yet little is known about their effects on fruit production and forest wildlife. We examined the effects of both single and recurrent wildfires on fruit production and large vertebrate abundance in a central Amazonian terra firme forest for 3 years following a large fire event. The estimated mortality of 42 and 74% of stems ≥ 10 cm in once- and twice-burnt forest led to a substantial loss of fruiting tree basal area (29 and 62% were lost in once- and twice-burnt forest, respectively) and crown coverage of fruiting woody lianas (89 and 97% were lost in once- and twice-burnt forest, respectively). Some important tree families producing fleshy fruits were less abundant than expected in once- and twice-burnt forest, suggesting that tree mortality was non-random in terms of species composition. Asynchronous fruit production was affected, and burnt forest transects sustained a much lower fruiting basal area, and fewer fruiting species during the dry season period of fruit scarcity. The number of fruiting trees in once- and twice-burnt forest was higher than the number predicted from actual levels of tree mortality recorded in each fire disturbance treatment, suggesting some surviving trees which may have benefited from higher irradiance levels and lower competition for resources. Many large frugivores and other vertebrate species declined in response to single fires, and most primary forest specialists were extirpated from twice-burnt forest, which sustained a higher number of species associated with second growth and other disturbed habitats.

Introduction

Frugivory and animal-mediated seed dispersal are important processes in tropical forests (Howe and Smallwood 1982; Howe 1986; Wilson 1989; Jordano 1992), and this is especially important in the neotropics, where up to 95% of plant species produce animal-dispersed fruits (Peres and Roosmalen 2002). By the same token, the neotropical flora is typically associated with a vertebrate fauna exhibiting a very high degree of specialisation for frugivory (Fleming et al. 1987). Forest disturbance events affecting fruit–frugivore interactions could thus have serious consequences for both tropical forest wildlife and floristic composition. Firstly, changes in fruit production can have effects on wildlife numbers, as most vertebrates are frugivorous to at least some degree (Emmons et al. 1983; Terborgh 1983; Janson and Emmons 1990) and

their abundance can be linked to fruit production (van Schaik et al. 1993). Secondly, large vertebrates have important influences on many forest trees, and changes in their abundance and assemblage composition could affect processes such as pollination, seed predation (Curran et al. 1999) and seed dispersal (Poulsen et al. 2002). While the effects of selective logging, forest fragmentation and hunting are becoming increasingly known, we focus on a new threat that has emerged in recent years – that of wildfires.

Soil and pollen records indicate that fires have been historically rare in Amazonian forests (Sanford et al. 1985; Turcq et al. 1998), and this is reflected by the fire-sensitive morphological characteristics of most trees (Uhl and Kauffman 1990; Barlow et al. 2003). Since fires associated with the 1982–1983 El Niño Southern Oscillation (ENSO) event first attracted scientific attention in the 1980s (e.g. Uhl and Buschbacher 1985; Leighton and Wirawan 1986; Woods 1989), fire has had dramatic impacts in large areas of tropical forests (Cochrane et al. 1999; Goldammer 1999; Nepstad et al. 1999; Cochrane 2001a; Siegert et al. 2001), even eroding the biodiversity value of national parks and other protected areas (Kinnaird and O'Brien 1998). Although the extent of these fires in Amazonia remains poorly understood, up to 1.5 million km² of forest may become flammable during severe ENSO-mediated droughts (Nepstad et al. 2001). Furthermore, fires are encouraged by forest fragmentation (Cochrane 2001b; Cochrane and Laurance 2002) and selective logging (Uhl and Buschbacher 1985; Nepstad et al. 1999; Siegert et al. 2001), and initial low-intensity surface fires can lead to more severe recurrent fires in subsequent dry seasons (Cochrane et al. 1999). Moreover, fires may become increasingly important in the more seasonal parts of Amazonia, especially if they are encouraged by the new wave of infrastructural development projects currently taking place (Laurance et al. 2001; Nepstad et al. 2001; Peres 2001).

At present, the ecological effects of tropical forest wildfires have been quantified in terms of tree mortality, forest structure, and the understory avian community structure (see Cochrane 2003; and Barlow and Peres 2004 for reviews). Apart from some information on mortality in the immediate aftermath of fires (e.g. Kinnaird and O'Brien 1998; Peres 1999a; Anggraini et al. 2000), and some qualitative reports following the 1982–1983 ENSO event, information on large vertebrates remains scarce and anecdotal (Barlow and Peres 2004a). Furthermore, despite several studies documenting assemblage-wide tree mortality, virtually nothing is known about the effects of fire disturbance on fruit production (but see Kinnaird and O'Brien 1998).

In this context, we examined the effects of single low-intensity and more severe recurrent wildfires on levels of fruit production and the abundance of large vertebrates in an Amazonian forest, 3 years after a wildfire burnt around 1140 km² of mostly forested land in the region (Nelson 2001). We use data from 44 0.25 ha tree plots and 16 km of fruit trails to quantify the effects of single and recurrent fires on aggregate fruit production from trees and woody lianas. We then examine three hypothesis as to how wildfires could affect vertebrate populations, and attempt to assess (1) whether key fleshy-fruit

bearing tree families are more likely to succumb to fire-induced mortality or losses in fruit crops than other plant taxa, (2) whether surviving trees were able to compensate for the loss of live trees by increasing fruit production, and (3) the effects of fire on year-round fruiting phenology in unburnt, once- and twice-burnt forest, and the extent to which fire-induced tree mortality either created or aggravated any background seasonal resource bottleneck. To examine the effects of fires on several groups of large vertebrates – all of which feed on fruit pulp to a greater or lesser extent – we include data from an unburnt unharmed control site 50 km upriver, and compare large vertebrate abundance following (i) hunting (but not fires), (ii) hunting and single burns, and (iii) hunting and recurrent burns.

Methods

Study site

This study took place in the hydrological catchment of the Rio Maró, a 3rd-order, clear-water tributary of the Amazon river. Fieldwork was carried out on both banks of the river, both within and outside the recently created Tapajós-Arapiuns Extractive Reserve of westernmost Pará, central Brazilian Amazonia (2°44' S, 55°41' W, see Barlow and Peres 2004a). This region is dominated by dense lowland ombrophilous forest (RADAM 1988), including primarily non-flooded (*terra firme*) forests, small enclaves of edaphic savannahs (*campinarana*) on white-sand soils, and narrow portions of flooded forest (*igapó*) along the Rio Maró. The climate is characterised by rainfall of 2041 mm yr⁻¹ [range = 1287–2538 mm yr⁻¹ (1992–1997); INFRAERO 1998] and a strongly demarcated dry season lasting 3–5 months (Peres et al. 2003).

A large swathe of forest in this area burnt in the period between October 1997 and January 1998 during a prolonged dry period resulting from the 1997–98 El Niño southern oscillation (ENSO) event. Fires in forests that were burning for the first time were characterised by low flame heights (usually 10–30 cm), although even these were sufficiently intense to burn the leaf litter and scorch the forest understorey to a height of approximately 2.5 m, leaving a few small (ca. 100 m²) unburnt patches where fuel conditions were unsuitable. Fires became much more intense when they entered forests that had already burnt within 10 years. Flames occasionally reached into the canopy, and no unburnt pockets were encountered within these forests.

Survey design

Tree mortality was assessed over an 8-month period from the end of August 2000 to May 2001, ≈3 years (32–41 months) after the most recent wildfires of December 1997–1998. Some areas affected by the 1997–1998 wildfire had

previously burnt during the 1988 ENSO event, and these are referred to hereafter as twice-burnt forest. Background levels of tree mortality were assessed by measuring and examining a total of 4798 standing stems ≥ 10 cm DBH in 44 0.25 ha (10×250 m) forest plots (16 in unburnt forest, 22 in once-burnt forest, and 6 in twice-burnt forest, see Barlow and Peres 2004a for plot locations and mortality data). These data were used to compare the abundance of live standing stems from different families across disturbance treatments, and to calculate the background changes in tree density across disturbance treatments.

Fruiting phenology and large vertebrate surveys were initiated in February 2001. Both fruit and animal surveys took place along five 4 km and two 5 km transects, located independently of existing trails which may have been used by hunters. Four transects were located in the lower Maró, and were placed in unburnt (transects Ufa and UFb), once-burnt (BF1) and twice-burnt (BF2) forest. All transects were cut in a straight line in a predetermined direction, regardless of atypical patches, treefalls or topography. Any bias in selecting forest types was minimised as the forests intercepted by these long transects were unknown when starting point and transect headings were decided. Although $n = 1$ for our two burnt treatments, each transect was long enough to capture a range of burn intensities, and the basal area within two 0.25 ha plots examined along each transects were within the typical range for each forest type (Figure 1). Less than 3% of the once-burnt transect intersected unburnt patches, and $< 8\%$ of the twice-burnt transect intersected forest that was estimated to have burnt only once. Data from all these patches was included in the analysis, as they were considered typical of that forest treatment.

Each transect was cleared of obstructions and regrowth vegetation every month, following each monthly vertebrate and fruit censuses. All lower Maró transects were 4 km in length. Additionally, one 4 km and two 5 km transects were cut in unburnt (UH) primary *terra firme* forest in a headwater tributary of the Rio Maró, 12 km upstream beyond the last extractive household (see Peres et al. 2003). Rainfall data was collected daily in the village of Cachoeira do Maró during the study. We also use a long-term rainfall data set obtained over 6 years (January 1992–December 1997) at Santarém airport (INFRA-ERO 1998), 110 km to the east of the study site.

Fruit surveys

The low density of live trees and dense understorey regeneration of burnt forest areas made any robust species-specific comparisons of fruiting activity extremely difficult. We also chose not to use 0.25 m² fruit traps, which would have been highly vulnerable to the stochastic presence or absence of individual trees in a flora composed of many rare and highly dispersed species (Pitman et al. 1999). Instead we adopted a variation of the terrestrial fruit trail technique, which provides results that are comparable to those of other methods

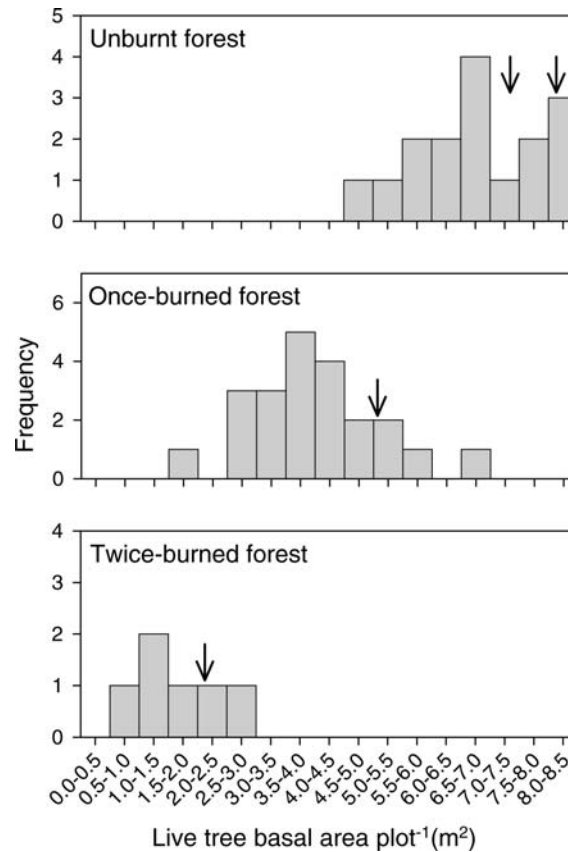


Figure 1. Frequency histograms of live basal area per plot (m^2) from 44 0.25 ha plots in unburnt ($n = 16$), once-burnt ($n = 22$) and twice-burnt forest ($n = 6$). Arrows indicate the mean of the two plots that were examined along each transect.

(Zhang and Wang 1995; Stevenson et al. 1998), and has the advantage of efficiently censusing a relatively large area of the forest, thus avoiding the chance concentration effect (Stevenson et al. 1998) and maximising the spatial variation (resulting from minor differences in topography and burn severity) captured within each disturbance treatment. For example, the total area surveyed ($16,000 \text{ m}^2$) is equivalent to that which could be sampled by 64,000 fruit-traps of 0.25 m^2 .

Each month, a 1-m wide strip of forest along each 4 km transect was carefully examined for fallen fruits. When a fruit patch was encountered along this strip, a voucher specimen was collected in order to aid identification, and the associated fruiting stem was identified by inspecting the spread of fallen fruits on the ground and the overhanging crowns with a pair of 10×40 binoculars. Once identified, the stem was measured (diameter at breast height, or above the

tallest buttress) and tagged, and stem size (basal area) was used as a widely validated correlate of fruit production (Leighton and Leighton 1982; Peters et al. 1988; Chapman et al. 1992; Stevenson et al. 1998). However, as basal area fails to consider multiple stems and is poorly correlated with fruit crop size in climbing plants (Chapman et al. 1994), crown spread was also estimated and crown coverage (m²) was used as the measure of fruit production in woody lianas. Although basal area can be inappropriate for examining fruit production in palms (Chapman et al. 1994; Stevenson et al. 1998), these comprised only 1.3% of fruiting trees and were included in the analysis of all fruiting trees.

Tree species were categorised into three functional groups according to whether seed dispersal was zoochorous (and then by whether they were either fleshy or sclerocarpic) or by abiotic means (combining autochorous and wind-dispersed seeds) on the basis of our own observations and the descriptions of fruits in van Roosmalen (1985) and Ribeiro et al. (1999).

Rates of fruit production relying on residual fruitfall may overestimate the degree of seasonality in fruit availability, as significant reductions in fruit production can increase the proportion of fruits and seeds removed by arboreal and terrestrial frugivores (Terborgh 1983; Zhang and Wang 1995). In a similar manner, it is possible that lower overall fruit production in burnt forest sites could have increased the proportion of fruits removed. However, fewer frugivores and seed predators in the burnt forest will have had a compensatory bias, decreasing the chance of fruit removal. As we were unable to predict the extent or direction of this bias, we minimised its effects by using tree size rather than fruit mass on the ground as our predictor of fruit production, and by examining the canopy for overhanging fruiting crowns even where non-edible fruit exocarps were the only remains of fruits detected within our 1-m wide strips. Possible overestimates of the duration of fruiting periods due to fruit persistence on the forest floor was prevented by only recording stems that retained fresh fruits in their crowns. Potential biases in search effort, detectability, and estimates of crown size were minimised by having a single observer.

Although general patterns in fruit phenology are often similar regardless of the methodology used (Zhang and Wang 1995; Stevenson et al. 1998), surveys relying on fruitfall generally show a 1 month lag when compared to fruit production estimates based on inspections of individual crowns (Zhang and Wang 1995; Wallace and Painter 2002) and our samples may have underestimated the onset of fruit production in the crown. Moreover, as the end of fruitfall periods was determined by crown inspections rather than fruits on the ground, the fruiting period of all stems may have been systematically underestimated by as long as 1 month. Finally, it should be noted that by only recording the presence or absence of fruits in the crown after the initial onset of fruiting, these data do not take into account potential changes in fruit crop size occurring before or after the initial detection of fruit on the trail.

Vertebrate censuses

Each lower Maró transect was walked twice each month for 14 months (February 2001–April 2002), resulting in 448 km of census effort (112 km per transect). The three upper Maró unburnt forest transects were walked in November and December 2000, accounting for a total of 142.6 km of outward (early morning) censuses (Peres et al. 2003). Return census walks conducted at the upper Maró site were excluded from this analysis to standardise the census methodology across all sites. All outward census walks were initiated at dawn (0600–0630 h) and terminated by mid-morning (ca. 1030 h), and were conducted at a slow pace (approximately 1300 m h⁻¹) following Peres (1999b). All large-bodied vertebrates encountered were recorded upon detection, along with time of day, group size, the detection cue (e.g. acoustic, visual), perpendicular distance from the transect, and distance along the transect. Indirect cues such as scrapes, tracks and faeces were also noted when they could be assigned to a particular species or genus. However, in most cases these indirect detection events were excluded from abundance estimates because some terrestrial species (such as brocket deer *Mazama* spp., cats, and armadillos) appeared to preferentially use trails cut within the dense understorey of burnt forest.

Census data were truncated to exclude all (mainly acoustic) detection events beyond perpendicular distances of 150 m from the trail, thus reducing the bias that can arise when comparing abundance data from censuses conducted in structurally different habitats (Johns 1985). Because sample sizes were small for many species, a simple encounter rate (detection events per 100 km walked) is used rather than population density estimates. Patterns of animal abundance presented here are unlikely to have been significantly influenced by intrinsic biases in detection probability. For example, similar trends in acoustic, olfactory and visual detection events were recorded in species such as howler monkeys, whilst there was no significant difference in the detection distance of species that were common in all habitats (e.g. detection distance of toucans, *Ramphastus tucanus* and *R. vitellinus*, and pigeons, *Columba subvinacea* and *C. plumbea* were not significantly different between unburnt forest and either once-burnt or twice burnt forest: Kolmogorov–Smirnov tests, $p = 0.3$ – 1.0 in all cases).

Data analysis

Chi-square tests were used to test for significant differences between disturbance treatments. Data from different transects in the same disturbance treatment were pooled together in order to maximise sample sizes. The expected frequencies that were used thus accounted for the sampling effort (i.e. the number of plots, the transect length, or the number of trees) allocated to each treatment. To incorporate levels of variation in fruiting tree basal area and fruiting liana crown area within forest types, data from transects were split

into 250 m sections, and compared using one-way ANOVA with Tukey's post-hoc test. All fruiting stems < 10 cm DBH were excluded from comparisons between the abundance of fruiting families between transects, thus maintaining consistency with data recorded in tree plots, and excluding the majority of pioneers that grew since the most recent fire event.

The % change (from unburnt forest) in live tree density and fruiting tree density in our burnt forest treatments was calculated using the mean of data from both unburnt forest transects as the baseline for fruiting trees, and the mean of data from the 16 unburnt 0.25 ha plots as the baseline for live tree density. The assumption that transects were typical of the plots measured within each forest treatment was assessed by comparing two 0.25 ha plots that were examined along each transect with the other 0.25 ha plots measured in that treatment (Figure 1). However, because there was considerable variation in tree density along transects, we use all 0.25 ha plots rather than the eight plots measured along the transects to estimate the change in background levels of tree density in once- and twice-burnt forest.

Results

Pre-burn forest similarity

Although we do not have an *a priori* experimental design, and fruit production and vertebrate abundance was only recorded along one transect in each of the burnt forest areas (reflecting the spatial extent of these fires, and the considerable logistical difficulties involved in cutting and maintaining viable trails within these habitats), we attribute most of our cross-site differences to the burn regime rather than to any pre-burn differences between transects. Interviews with local peoples and personal observations confirmed that the sites sampled had been similar in terms of soil types, species composition, forest structure and hunting pressure prior to fires, while mean basal area from two 0.25 ha plots examined along each transect were within the range of the other plots examined within each treatment (Figure 1). Furthermore, there was a similar pattern of dominance at the level of fruiting tree and liana genera (J. Barlow, unpubl. data), and vertebrate species (Table 4), across the two unburnt forest samples (69.3 and 85.1% similarity between the two transects respectively, using the Bray–Curtis similarity measure on the untransformed data of fruiting trees and large vertebrates), which were on opposite banks of the river and located as far from one another as they were from the burnt forest transects.

Fruiting tree abundance

Total fruiting tree abundance was considerably lower in once-burnt and twice-burnt forest transects than in the two unburnt forest transects (Figure 2). The

mean fruiting basal area declined similarly, and in once- and twice-burnt forest comprised 71 and 38% of the mean unburnt forest level, respectively. Fruiting lianas were much less abundant than fruiting trees in all habitats, accounting for only 10, 7 and 5% of fruiting stems in unburnt, once- and twice-burnt forest, respectively. The high mortality rate of large woody lianas resulted in the collapse of fruiting liana crown coverage, which comprised only 11 and 3% of the mean unburnt forest level in once-burnt and twice-burnt forest, respectively (Figure 2).

When all stems are grouped by their DBH size class, the sharp decline in numbers of fruiting trees in twice-burnt forest was evident across all tree size classes ≥ 10 cm DBH. In contrast, small fruiting stems (< 10 cm DBH) were most abundant in twice-burnt forest (Figure 3), although this difference was not significant. Compensation, from the rapid growth of fruiting stems

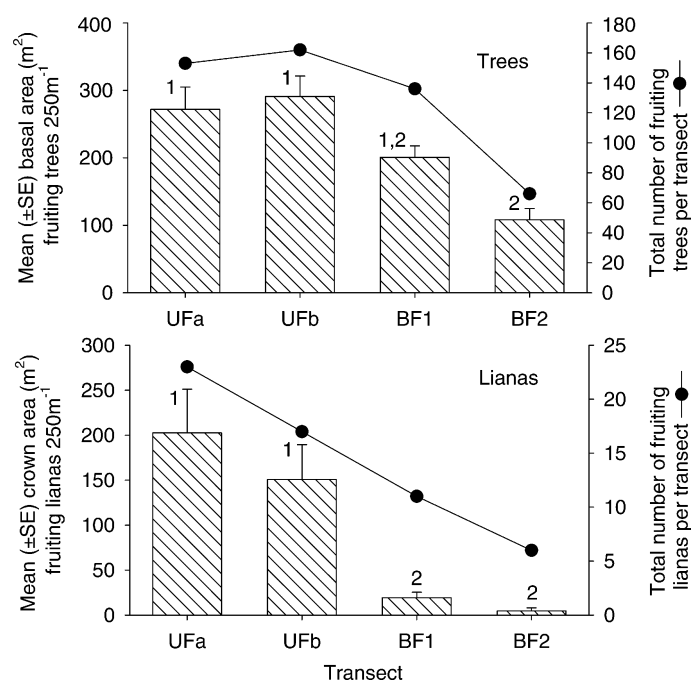


Figure 2. Abundance of fruiting stems recorded during the 14 month fruit surveys along each of the four 4-km transects, which were placed in unburnt forest (Ufa and Ufb), once-burnt forest (BF1) and twice-burnt forest (BF2). Bars indicate either mean (\pm SE) basal area (trees) or mean (\pm SE) crown area (lianas), with means generated from 250 m sections ($n = 16$ for each transect). Closed circles indicate total number of fruiting stems recorded in each transect. There were significant differences in the mean fruiting basal area/crown area per transect, and the total number of fruiting trees/lianas per transect (fruiting trees; basal area, $F_{3, 60} = 10.6$, $p < 0.001$; number of stems, $\chi^2 = 44.0$, d.f. = 3, $p < 0.001$; fruiting lianas; crown area, $F_{3, 60} = 9.8$, $p < 0.001$; number of stems, $\chi^2 = 11.4$, d.f. = 3, $p < 0.025$). Numbers above bars indicate Tukeys subsets for ANOVAs.

< 10 cm DBH into the 10–19.9 cm DBH size class, and the apparent increase in the fruiting activity of some fruiting families (Table 2), meant that fires appeared to have had minimal effects on the number of fruiting trees < 30 cm DBH in once-burnt forest, despite high rates of post-fire tree mortality in these size classes. However, large stems (≥ 40 cm DBH) were much less abundant in once-burnt than in unburnt forest (Figure 3).

Live tree abundance and fruit production

The percentage decline in fruiting trees ≥ 10 cm DBH within once-burnt ($p < 0.001$) and twice-burnt ($p < 0.05$) forest was lower than the percentage decline in live trees (including pioneers) estimated by comparing tree density in the 22 once-burnt and six twice-burnt 0.25 ha plots with tree density in the 16 0.25 ha unburnt forest plots (Figure 4). Trees from the size classes 10–19.9 cm DBH were recorded bearing fruit more often than would be expected from their background densities in both once-burnt and twice-burnt forest ($p < 0.001$), while fruiting trees 30–39.9 cm DBH fruited more than expected in once-burnt forest ($p < 0.01$; Figure 4).

Considering live stems ≥ 10 cm DBH in the most abundant tree families, Burseraceae, Lecythidaceae, Humiriaceae and Violaceae trees were all significantly less abundant in the once-burnt forest plots than expected from the overall live tree density in this forest treatment. Of these families, only Burseraceae and Violaceae were also significantly less abundant in twice-burnt forest, and the

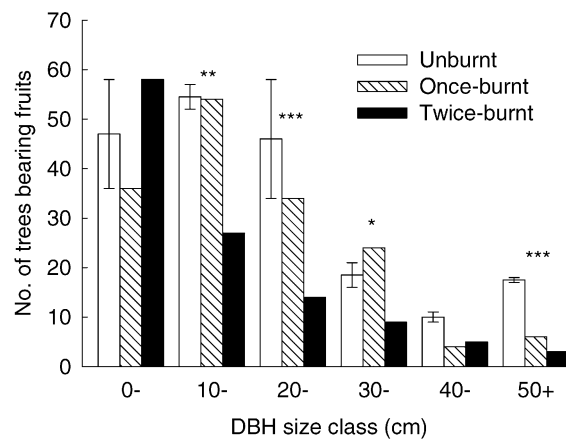


Figure 3. Number of fruiting trees in different size classes in each disturbance treatment. Unburnt forest bars and error bars represent the mean and range of both control transects (Ufa and Ufb). Significance was calculated using chi-square, using expected frequencies generated from the length of transect examined in each disturbance treatment (d.f. = 2). * $p < 0.05$, ** $p < 0.005$, *** $p < 0.001$.

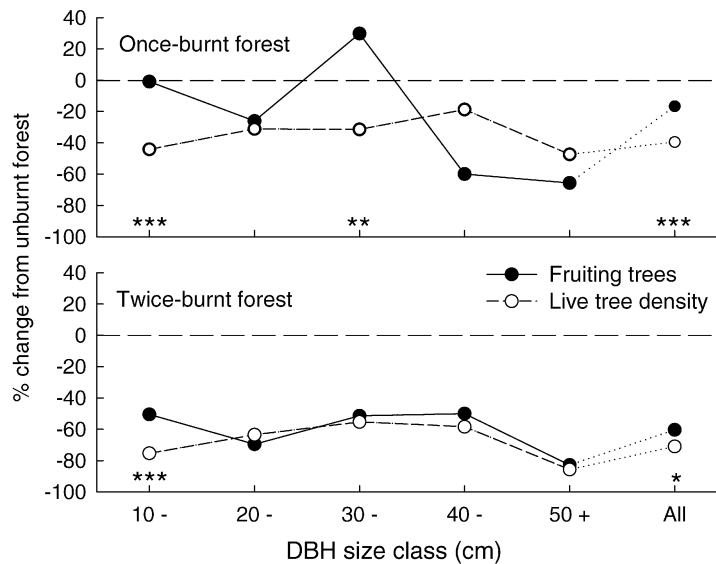


Figure 4. Percentage change (from their respective levels in unburnt forest) in the abundance of live trees (from plot data) and trees bearing fruit (from transect data) in once- and twice-burnt forest. Trees are grouped by DBH size classes, and chi-square tests (d.f. = 1) were used to examine whether the number of fruiting trees in each size class, and in each disturbance treatment, was significantly more or less than the number that would be expected if fruiting trees along transects declined by the same amount as live trees in the 0.25 ha tree plots. * $p < 0.05$, ** $p < 0.005$, *** $p < 0.001$.

latter (predominantly *Rinorea* sp.) had apparently been extirpated by recurrent fire disturbance. Sapotaceae and Myristicaceae trees comprised a smaller proportion of the trees in twice-burnt forest plots than expected from those in unburnt forest. Palm (Arecaceae) density remained unaffected by fire disturbance, so they comprised a significantly greater proportion of live trees in once- and twice-burnt forest than in unburnt forest (Table 1).

Seven of the 12 most abundant tree families in the 44 0.25 ha forest plots sampled were also among the 12 top-ranking families producing fruit along the four census transects (Table 2). Considering all trees bearing fruits, only those in the family Burseraceae were significantly less abundant than expected (relative to the decline of all fruiting stems) along transects in both types of burnt forest. Both Melastomataceae and Annonaceae stems fruited more often than expected along the once-burnt forest transects, although they did not deviate significantly from their expected level in twice-burnt forest. The observed increase of these families in once-burnt forest is best attributed to an increase in fruit production per stem rather than any pre- or post-fire difference in stem abundance, as their live stem densities in once-burnt forest were actually marginally (but not significantly) lower than in unburnt forest (mean \pm SE number of stems per plot; for Annonaceae, unburnt = 6.4 ± 0.8 , once-burnt =

Table 1. Density of live stems (per hectare) of the 12 most abundant tree families within 0.25-ha plots in each forest disturbance treatment.

	Total no. of stems recorded	Stems ha ⁻¹			UF-BF1		UF-BF2	
		UF ^a	BF1 ^a	BF2 ^a	Obs/exp	χ^2	Obs/exp	χ^2
Sapotaceae	479	62	42	2	1.08	2.4	0.13	18.4***
Burseraceae	445	66	32	4	0.89	4.7*	0.25	15.2***
Leg. Caesalpinaceae	325	40	28	7	1.09	2.2	0.65	2.0
Arecaceae	231	23	19	23	1.21	6.9**	3.12	55.4***
Anonaceae	224	26	20	8	1.15	3.8	1.16	0.3
Lecythidaceae	175	29	9	6	0.67	14.4***	0.80	0.5
Lauraceae	160	22	12	5	0.95	0.3	0.82	0.3
Leg. Papilionoidae	159	19	13	9	1.10	1.2	1.67	3.8
Leg. Mimosoidae	156	19	14	3	1.11	1.5	0.69	0.8
Humiriaceae	132	20	7	8	0.73	7.3**	1.44	1.8
Myristicaceae	126	19	9	1	0.85	2.4	0.28	4.0*
Violaceae	95	20	3	0	0.40	27.8***	0.00	7.7**
All live tree stems	3700	484.5	285.6	127.3				

Once-burnt (BF1) and twice-burnt forest (BF2) plots were compared with unburnt forest (UF) using chi-square tests (d.f. = 1). To account for differences in overall live tree density and sample effort, tests used an expected frequency that corrected for the total number of stems recorded in each habitat. Obs/exp shows the ratio between the observed and the expected values in each burnt treatment.

* < 0.05, ** < 0.005, *** < 0.001.

^aOriginal values used in the chi-square tests can be obtained by multiplying values per hectare by 4, 5.5 and 1.5 in UF, BF1 And BF2 respectively.

5.0 ± 0.7 ; $Z = 1.6$, $p = 0.11$; for Melastomataceae, unburnt = 2.9 ± 1.0 , once-burnt = 1.6 ± 0.5 ; $Z = 1.2$, $p = 0.28$). Although most other families were too rare to warrant comparisons, some of the trends complement the significant results from live tree densities, and fruiting palms were most abundant along burnt forest transects, and Myristicaceae stems were least abundant in twice-burnt forest (Table 2).

Fruiting phenology

Fruiting phenology was strongly associated with the seasonal pattern of rainfall in the region across all forest treatments (Figure 5), and with the exception of the aggregate crown area of lianas in twice-burnt forest, all groups in all transects were significantly and positively correlated to either (or both) the monthly rainfall averages from Santarém and/or the monthly rainfall recorded locally during the 14 months of study (J. Barlow, unpubl. data). Although once-burnt and twice-burnt forest had a slightly higher abundance of fruiting stems in September (the month of lowest overall fruit availability), the overall species richness of fruiting stems over the four dry-season months was far lower than that in unburnt forest (Table 3), and in once-burnt forest was

Table 2. Total number of fruiting stems ≥ 10 cm DBH along each transect for the 12 most abundant tree families.

	Total no. of stems recorded	Stems transect ⁻¹				UF-BF1		UF-BF2	
		UFa	UFb	BF1	BF2	Obs/exp	χ^2	Obs/exp	χ^2
Burseraceae	139	51	62	16	10	0.42	18.2***	0.50	6.1*
Anonaceae	73	15	14	36	8	1.87	20.9***	1.32	0.7
Sapotaceae ^a	34	10	13	4	7	0.50	2.8	1.42	1.1
Melastomataceae ^a	30	3	8	17	2	2.06	13.1***	0.94	0.0
Myrtaceae ^a	22	7	7	8	0	1.23	0.5	0.00	2.7
Leg. Caesalpinaceae	18	8	3	5	2	1.06	1.7	0.94	–
Myristicaceae	12	6	2	3	1	0.92	–	0.68	–
Chrysobalanaceae	11	3	0	4	4	1.93	–	3.49	–
Leg. Mimosoidae	11	7	2	1	1	0.34	–	0.61	–
Moraceae	10	4	2	4	0	1.35	–	0.00	–
Arecaceae	8	1	0	3	4	2.54	–	4.88	–
Malphiaceae	8	0	3	2	3	1.35	–	3.05	–
All fruiting trees	470	140	151	122	57				

Once-burnt (BF1) and twice-burnt forest (BF2) transects were compared with the unburnt forest treatment (UFa and UFb) using chi-square (d.f. = 1). To account for differences in fruiting stem density, tests used an expected frequency corrected for the number of fruiting trees ≥ 10 cm DBH recorded in each treatment (see totals). Obs/exp shows the ratio between the observed and the expected values in each burnt treatment.

Probability values: * < 0.05, ** < 0.005, *** < 0.001. '–' No test performed, expected values < 4.5.

^aExpected values fell below 5 (but > 4.5) for UF-BF2 comparison.

almost entirely dominated by *Bellucia* spp. In fact, the number of fruiting *Bellucia* stems ≥ 10 cm DBH was significantly higher in once-burnt than in unburnt forest ($\chi^2 = 7.8$, d.f. = 1, $p < 0.001$), even though (like all Melastomataceae stems) there was no significant difference in the abundance of live *Bellucia* stems between 16 unburnt and 22 once-burnt forest plots (mean \pm SE stems per plot in unburnt forest = 0.88 ± 0.35 ; in once-burnt forest = 0.59 ± 0.21 ; $Z = -0.54$, $p = 0.7$).

Large vertebrates

A total of 50 large-bodied vertebrate taxa (including species identified only to the level of genera) were recorded along the 590.6 km of transect walks. Independently of fires, hunting pressure had significantly reduced the abundances of five of the 17 species common enough to allow statistical comparisons between unburnt and hunted unburnt forest. These included brown capuchins *Cebus apella*, agoutis *Dasyprocta agouti* and tortoises *Geochelone* spp.

Most species declined in abundance 3 years after the single-fire event (Table 4). Of the 27 species sufficiently abundant to warrant statistical comparisons, 14 declined, two (little tinamou *Crypturellus soui* and the red-necked aracari *Pteroglossus bitorquatus*) increased, and nine showed no

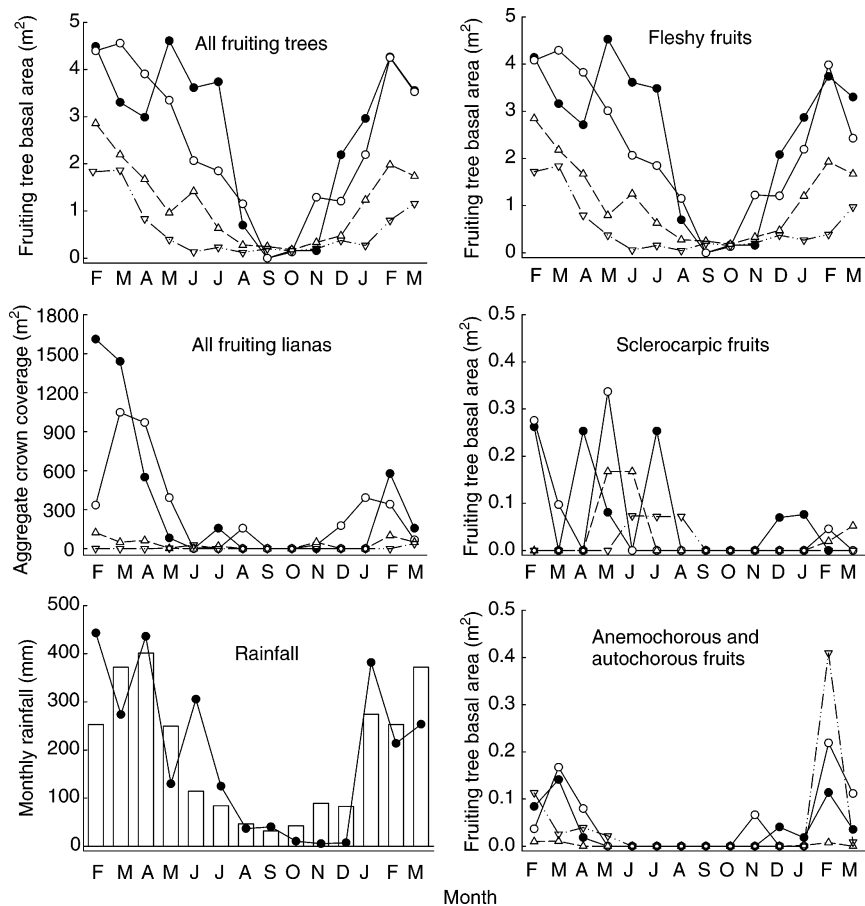


Figure 5. Seasonal patterns of fruit production along the four forest transects. Unburnt transects are indicated by solid lines and either solid (Ufa) or open (Ufb) circles. Once- and twice-burnt forest transects are indicated by dashed lines with grey up-pointed triangles (BF1), and dot-dash lines with open down-pointed triangles (BF2), respectively. Rainfall graph shows monthly rainfall over a 6-year period in Santarém (clear bars) and the monthly rainfall sampled at the study site during the study period (closed circles and line).

significant changes. The more severe recurrent fire caused increasing levels of faunal impoverishment, and some species that initially persisted in once-burnt forest were extirpated from the areas that had burnt twice. Moreover, the six species that either increased significantly (Hoffman's titi monkey *Callicebus hoffmannsi*, tassel-eared marmoset *Callithrix humeralifera* and *Crypturellus soui*) or were most abundant (squirrel monkey *Saimiri ustus*, speckled chachalaca *Ortalis guttata* and black-necked Aracari *Pteroglossus aracari*) in twice-burnt forest were also associated with second-growth forests throughout the region (J. Barlow, pers. obs.). There was also a slight trend towards smaller

Table 3. Number of stems of tree genera bearing fruits along each transect during the 4 dry season months (August–November).

Family	Genus	UFa	UFb	BF1	BF2
Anarcardiaceae	<i>Spondias</i> spp.	0	1	1	0
Annonaceae	Unidentified	1	0	0	0
Arecaceae	<i>Attalea</i> spp.	0	0	0	1
Clusiaceae	<i>Clusia</i> spp.	0	1	0	0
Combretaceae	<i>Buchenavia</i> spp.	0	1	0	0
Humiriaceae	<i>Sacoglottis</i> spp.	0	0	0	2
Humiriaceae	Not identified	0	1	0	0
Leg. Mimosoideae	<i>Inga</i> spp.	1	0	0	0
Leg. Caesalpinjiaceae	<i>Sclerolobium</i> spp.	0	1	0	0
Melastomataceae	<i>Bellucia</i> spp.	0	3	5	1
Myristicaceae	<i>Virola</i> spp.	1	0	0	0
Sapindaceae	<i>Toulicia</i> and <i>Talisia</i> spp.	1	0	0	0
Sapotaceae	Unidentified	1	1	1	0
Tiliaceae	<i>Apeiba</i> spp.	1	0	0	0
Unidentified	Unidentified	0	2	1	0
Species richness		6	8	4	3
Aggregate basal area (m ²)		0.86	2.36	0.35	0.43

group sizes among primate species persisting in the burnt forest (Table 5), although in most cases sample sizes were very small within at least one of the disturbance treatments.

Discussion

Pre-existing differences between transects

Although pre-existing differences between transects could explain some of the variation observed in these results, we consider fire history as the most parsimonious explanation for the vast majority of differences between treatments. Firstly, the scale of the differences found between our burnt transects and the unburnt transects were considerably greater than those observed between our two unburnt transects (Figures 2 and 5, Table 2). Secondly, the generality of these results was supported by tree data from our 44 0.25 ha tree plots (Table 1), and the mean basal areas from two 0.25 ha plots that were examined along each transect were within the typical range for each forest treatment (Figure 1). Finally, the long lengths of our transects ensured a variety of topographies and levels of burn severity were captured in each sample.

Spatial and temporal patterns of fruit production

As phenological patterns of fruit production in tropical forests can be subject to relatively high levels of variation between years (Wallace and Painter 2002)

Table 4. Number of animals (or groups in social species) detected per 100 km walked.

	Detection events per 100 km walked					Comparisons between disturbance groupings (χ^2)						
	Unhunted and unburnt (UH)	Hunted and unburnt (UFa)	Hunted and unburnt (UFb)	Hunted and once-burnt (BF1)	Hunted and twice-burnt (BF2)	Unhunted-hunted	Hunted-hunted once-burnt	Hunted-hunted twice-burnt	Comparisons between disturbance groupings (χ^2)			
									once-burnt	twice-burnt		
Mammals												
Primates												
<i>Alouatta belzebul</i> ^a	26.6	46.4	28.6	17.0	8.0	↔ns	↓**	↓***	↔ns	↓***	↓***	↓***
<i>Calliebus hoffmannsi</i>	6.3	1.8	0.9	3.6	7.1	↓**	↑	↑***	↓	↑***	↑***	↑***
<i>Callithrix humeralifera</i>	17.5	0.0	0.9	1.8	8.0	↓***	↑	↑***	↓	↑***	↑***	↑***
<i>Cebus albifrons</i>	4.9	8.9	2.7	0.9	0.0	↔ns	↓*	↓**	↔ns	↓**	↓**	↓**
<i>Cebus apella</i>	21.0	8.9	4.5	4.5	3.6	↓***	↓	↔ns	↔ns	↔ns	↔ns	↔ns
<i>Chiropotes albinasus</i>	3.5	0.0	1.8	0.0	0.0	↓	↓	↓	↔ns	↔ns	↔ns	↔ns
<i>Pithecia irrorata</i>	7.0	6.3	6.3	8.0	0.0	↔ns	↔ns	↔ns	↔ns	↔ns	↓**	↓**
<i>Saimiri ustus</i>	0.0	0.0	0.0	0.0	4.5	abs	abs	abs	abs	abs	↑	↑
Ungulates												
<i>Mazama gouazoubira</i>	3.5	2.7	0.0	0.0	0.0	↓	↓	↓	↓	abs	abs	abs
<i>Mazama americana</i>	2.1	4.5	5.4	0.9	1.8	↑ns	↓*	↓*	↓*	↓ns	↓ns	↓ns
<i>Mazama</i> spp. ^b	5.6	7.1	6.3	0.9	1.8	↔ns	↓**	↓**	↓**	↓ns	↓ns	↓ns
<i>Tayassu pecari</i>	1.4	0.0	0.0	0.0	0.0	↓	abs	abs	abs	abs	abs	abs
<i>Tayassu tajacu</i>	0.5	1.8	0.9	0.0	1.8	↑	↓	↓	↓	↔	↔	↔
<i>Tapirus terrestris</i>	1.4	0.0	0.0	0.0	0.0	↓	abs	abs	abs	abs	abs	abs
Rodents												
<i>Sciurus</i> spp.	6.3	6.3	3.6	1.8	0.9	↔ns	↓ns	↓ns	↓ns	↓ns	↓ns	↓ns
<i>Dasyprocta agouti</i>	138.1	16.1	29.5	8.9	7.1	↓***	↓**	↓**	↓**	↓**	↓**	↓**
Edentates												
<i>Dasypus</i> spp. ^c	–	8.0	14.3	5.4	5.4	–	↓ns	↓ns	↓ns	↓ns	↓ns	↓ns
<i>Prionomys maximus</i>	0.7	0.9	1.8	0.0	0.0	↔	↔	↔	↔	↔	↔	↔
<i>Tamandua tetradactyla</i>	1.4	0.0	0.9	0.0	0.0	↓	–	–	–	–	–	–
<i>Myrmecophaga tridactyla</i>	0.5	0.0	0.9	0.0	0.0	–	–	–	–	–	–	–

Table 4. (Continued)

	Detection events per 100 km walked				Comparisons between disturbance groupings (χ^2)			
	Unhunted and unburnt (UH)	Hunted and unburnt (UFa)	Hunted and unburnt (UFb)	Hunted and once-burnt (BF1)	Hunted and twice-burnt (BF2)	Unhunted-hunted	Hunted- once-burnt	Hunted- hunted and twice-burnt
<i>Pyrrhura rhodogaster</i>	–	7.1	6.3	7.1	1.8	–	↔ns	↓ns
Other birds	–	–	–	–	–	–	–	–
<i>Columba</i> spp.	–	140.2	122.3	106.3	92.9	–	↓ns	↓**
<i>Daptrius americanus</i>	2.1	5.4	5.4	0.9	0.0	↑ns	↓*	↓*
<i>Gymnostinops</i> and <i>Psarocolius</i> spp.	–	39.3	23.2	4.5	4.5	–	↓***	↓***
<i>Geotrygon montana</i>	–	43.8	52.7	20.5	–	–	↓***	–
<i>Odontophorus gujanensis</i>	4.2	0.9	0.0	0.9	0.0	↓	–	–
<i>Psophia viridis</i>	15.4	13.4	5.4	0.0	0.0	↔ns	↓**	↓**
Reptiles	–	–	–	–	–	–	–	–
Geochelone spp.	22.4	0.9	0.0	0.0	0.0	↓***	–	–
Other	–	–	–	–	–	–	–	–
Army ant-swarms	–	1.8	6.3	2.7	3.6	–	↔nsc	↔nsc

All detection data are truncated at perpendicular distances of 150 m. Numbers shown are from visual or acoustic detections unless stated otherwise. '↓' in a data column indicates that data were not obtained for this species within that disturbance treatment. Data from the two hunted and unburnt transects were pooled together to increase sample sizes, and expected frequencies were calculated from the census distance walked within each disturbance type (d.f. = 1 for all tests). χ^2 tests used an expected frequency corrected for the distance walked in each disturbance treatment. Where χ^2 tests were performed, ns = no significant change, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, and arrows indicate the direction of change. Where tests could not be carried out, ↓ = declines of $\geq 50\%$, and ↑ = increase of $\geq 100\%$; ↔ no change; – fewer than 3 detection events in comparison; abs = absent from both categories.

^aIncludes olfactory detections of faeces and urine.

^bIncludes visual detections of faeces.

^cIncludes freshly excavated scrapes.

^dExcludes 8 additional sightings made beyond 4 km along the 5 km unburnt and unburnt forest transects (therefore negating the potential influence of time of day).

Table 5. Average group sizes (ags) and the number of visual detections (*n*) of the most abundant group-living species at each of the four lower Maró transects.

	Ufa		UFb		BF1		BF2	
	ags	<i>n</i>	ags	<i>n</i>	ags	<i>n</i>	ags	<i>n</i>
Primates								
<i>Alouatta belzebul</i>	5.1	(15)	5.1	(11)	4.0	(5)	4.0	(1)
<i>Callicebus hoffmannsi</i>	3.0	(1)	0.0	(0)	3.5	(2)	4.3	(4)
<i>Callithrix humeralifera</i>	0.0	(0)	8.0	(1)	6.5	(2)	5.3	(8)
<i>Cebus albifrons</i>	19.6	(9)	19.0	(3)	4.0	(1)	0.0	(0)
<i>Cebus apella</i>	15.4	(9)	14.3	(4)	12.5	(4)	8.0	(4)
<i>Pithecia irrorata</i>	4.6	(7)	4.3	(6)	3.1	(7)	0.0	(0)
Birds								
<i>Amazona</i> spp.	4.5	(6)	6.5	(2)	3.0	(2)	2.7	(3)
<i>Deropterus accipitrinus</i>	3.3	(3)	1.0	(1)	6.0	(1)	12.0	(1)
<i>Gymnostinops</i> and <i>Psarocolius</i> spp.	1.6	(9)	2.8	(4)	0.0	(0)	0.0	(0)
<i>Penelope pileata</i>	2.0	(2)	1.8	(5)	2.0	(1)	0.0	(0)
<i>Penelope superciliosus</i>	2.2	(14)	2.0	(10)	1.9	(11)	1.8	(8)
<i>Psophia viridis</i>	12.2	(9)	11.5	(4)	0.0	(0)	0.0	(0)
<i>Pteroglossus bitorquatus</i>	0.0	(0)	2.0	(1)	1.9	(7)	2.0	(1)
<i>Pyrrhura rhodogaster</i>	5.3	(6)	3.7	(3)	4.3	(4)	5.5	(2)
<i>Ramphastus tucanus</i>	3.0	(3)	1.0	(2)	1.6	(7)	4.0	(3)
<i>Ramphastus vitellinus</i>	1.8	(4)	1.0	(1)	3.0	(7)	2.5	(4)

and across relatively small spatial scales (Chapman et al. 1999a), these data should only be seen as a snapshot of phenological patterns and fruit production in the three disturbance treatments. However, these results do provide evidence of a strong association between fruit production and a sharply demarcated dry season (cf. Terborgh 1983; Peres 1994), contrasting with other tropical forests where rainfall is considered to be a poor predictor of seasonal fruit production (Putz 1979; Chapman et al. 1999a; Wallace and Painter 2002). Although fruiting patterns were most clearly marked among taxa bearing fleshy fruits (Figure 5), which may require high moisture levels for fruit production (Lieberman 1982; Rathke and Lacey 1994), other types of fruit showed similar seasonal trends.

Potential effects of fruit-crop losses for large frugivores

The considerable loss of fruiting basal area in burnt forest reflects the high overall tree mortality observed following both single and recurrent fires (Cochrane and Schulze 1999; Slik and Eichhorn 2003; Barlow and Peres 2004a), while the collapse in liana crown coverage supports other studies suggesting that woody lianas are highly susceptible to fires (Gerwing 2002; Peres et al. 2003). As the abundance of tropical forest frugivores can be linked to fruit production (such as Chapman et al. 1999b; Balcomb et al. 2000;

Stevenson 2001), fire-induced mortality of trees and lianas bearing fleshy fruits should reduce the abundance of generalist frugivores. However, simple estimates of tree mortality and fruit production could mask more complex effects of fire disturbance, and we therefore examine three scenarios where fire-induced changes in fruit availability could differ from the background rate of tree mortality.

Non-random tree mortality

Tree mortality following fires is affected by morphological traits such as bark thickness and the presence of buttresses (Uhl and Kauffman 1990; Barlow et al. 2003), and the two families of trees that showed greater than expected post-fire numeric declines (Burseraceae and Sapotaceae) also frequently exhibited morphological traits associated with fire-intolerance. For example, measurements from eight 0.25 ha unburnt forest plots where tree morphology was examined (see Barlow et al. 2003) showed that buttresses were common in both families (accounting for 83 and 62% of stems ≤ 10 cm DBH in Burseraceae and Sapotaceae, respectively, as opposed to 41% for the entire tree assemblage), and both were associated with thin bark (4.0 ± 2.6 mm and 4.4 ± 2.7 mm for stems ≥ 10 cm DBH in Burseraceae and Sapotaceae, respectively, compared with 5.5 ± 1.3 mm for all trees). The significance of the decline in Burseraceae trees was also supported by lower than expected numbers of fruiting stems in this family along burnt forest transects. As these two families represented 36% of all fruiting trees in unburnt forest, and are important food sources for both primates and birds (van Roosmalen 1985; Ribeiro et al. 1999), their vulnerability to fire supports earlier interview-based evidence that suggested that post-fire declines in frugivore populations resulted from the high mortality of key food species (Peres et al. 2003).

Inconsistencies in the significant responses of other tree families make them more difficult to interpret in the absence of pre-burn abundance data. For example, although the Lecythidaceae and Humiriaceae were less abundant than expected in once-burnt forest, they did not show a significant response to twice-burnt forest, which may suggest that differences in their abundance levels in once-burnt forest may have been due to factors other than fire disturbance. However, the resilience of palms (Arecaceae) is exactly what would be predicted from the morphological characteristics of their transport system, as their phloem and xylem vessels run throughout their stems and are therefore well protected from transient heat stress (Gill 1995).

Non-lethal fire effects

It could be hypothesised that many trees surviving fires would reduce or abort fruit production due to partial stem damage inducing post-fire stress. However, assuming the live tree-density along our transects reflected the number of live trees recorded in the 44 0.25 ha plots, then fruit production in once- and twice-burnt forest was greater than was expected for certain size classes. Although this may be partially accounted for in the 10–20 cm size class by the rapid

regeneration of pioneers, the influence of this is small, as very few pioneer species had actually reached this size. Moreover, some families such as Melastomataceae and Annonaceae fruited at double the expected rate in once-burnt forest, even though our tree plots suggested they were no more abundant within that habitat than in unburnt forest. Fire-enhanced fruit production is a common phenomenon in many North American and Australian fire-climax ecosystems (Kauffman and Uhl 1990), and it seems likely that it could also occur in disturbed tropical forests as a result of increased irradiance levels, lower competition with other trees, or any post-fire nutrient flush. Although a similar response was only documented in one out of 14 species investigated in Amazonian forest edges (Laurance et al. 2003), it has been noted in logged Malaysian dipterocarp forests (Johns 1988), and may be a potential buffer protecting frugivorous species against the loss of canopy food sources (Chivers 1972).

Asynchronous fruit production

All other things being equal, the probability of periods of fruit scarcity occurring in seasonal environments will increase as the live stem density decreases, and the lower species richness and aggregate basal area of trees fruiting asynchronously along once- and twice-burnt forest transects indicated that fires did increase the severity of the seasonal resource bottleneck. However, this reduction was partially offset by an increase in the fruiting of key food species such as *Bellucia*, which are known to be important for some primates during periods of fruit scarcity (Wallace 1998; T. Haugaasen, pers. comm.). This compensation meant that during the month of greatest fruit scarcity (September) the basal area producing ripe fruits was marginally higher within both types of burnt forest than it was in unburnt forest (Figure 5). Furthermore, palms have been proposed as an important keystone resource (Terborgh 1986, but see Galleti and Aleixo 1998), and not only was their live stem density unaffected by fires (Table 1), they were actually recorded as fruiting more frequently in burnt forest than in unburnt forest (Table 2).

In summary, although these data suggest that some key fruit-bearing tree families were particularly vulnerable to fires, this may have been partially offset in once-burnt forest by the compensatory fruiting by some genera of surviving trees. Furthermore, as some of these genera also fruited during the fruit scarcity period, changes to the seasonal resource bottleneck were less severe than expected. However, the dramatic reduction in total fruiting stem density is likely to have an effect regardless of any compensatory or seasonal responses. In addition, the reduction in fruit availability could have effects beyond the simple loss of food resources: A lower density of fruit patches will force frugivores to allocate more time and energy in search and travel, whilst larger foraging aggregations converging upon a smaller number of fruit patches could affect the intensity of interference competition, and render animals more vulnerable to hunters (Lambert and Collar 2002).

Direct effects of fires on large vertebrates

The short-term pattern of faunal shifts indicated by Peres et al. (2003) were generally supported by these extended surveys. As predicted by Peres et al. (2003), we noted reductions in the abundance of specialised seed predators such as parrots (*Amazona* spp. and *Derophtyus accipitrinus*) and macaws (*Ara* spp.), and ripe-fruit specialists (such as white-crested guan *Penelope pileata* and white-fronted capuchin *Cebus albifrons*). Moreover, the overall predicted trend towards the increasing 'secondarisation' of the burnt forest vertebrate fauna was supported in this study, and there was a strong association between the use of second-growth (*capoeiras*) by different species and their occurrence in burnt forest (J. Barlow, pers. obs).

However, there are some noteworthy contrasts between these results and our results based on interviews with local people (Peres et al. 2003). Primate species dependent on fruits such as brown capuchins *Cebus apella* and saki monkeys *Pithecia irrorata* were more resilient to single-fires than was indicated by interviewees, whereas others able to resort to foliage, such as howler monkeys *Alouatta belzebul*, appeared to be less tolerant of fires than anticipated. Furthermore, the widely reported resilience of terrestrial browsers (see Barlow and Peres 2004a) was not apparent in our surveys, and both species of brocket deer (*Mazama americana* and *M. gouazoubira*) appeared to decline following single fires. It is likely that these discrepancies stem from the restricted knowledge of local peoples during the interviews, as the dense and impenetrable understorey regeneration prevented most of them from entering the forest to hunt 1 year after the fire.

As the abundance of forest vertebrates can be affected by fruit availability throughout the humid tropics (Chapman et al. 1999b; Balcomb et al. 2000; Stevenson 2001; O'Brien et al. 2003), it is tempting to associate the decline in many frugivorous species solely to the loss of fruit production. However, fires also had huge impacts on forest structure, which can also affect frugivorous species (Nogales et al. 1999; Terborgh and Petren 1991). The low canopy tree density in twice-burnt forest could be a barrier to the movement of large arboreal species (perhaps explaining the vulnerability of some of the large-bodied non-volant vertebrates), while others could be discouraged by a real or perceived risk of predation (Howe 1979). Rather than being associated with dietary guilds, the emerging pattern appears similar to that found in understorey insectivorous birds (Barlow et al. 2002), where fire disturbance favours generalist species adapted to second-growth and forest edges to the detriment of habitat specialists.

As some of the endemic primate species with the most restricted ranges (e.g. *Callithrix humeralifera* and *Callicebus hoffmannsi*) can be abundant in second-growth, they were also tolerant of changes in habitat structure and fruit production induced by wildfires. However, fires remain a threat to fire-intolerant, regionally endemic species such as white-nosed bearded saki *Chiropotes albinasus* and *Penelope pileata* whose distributions coincide with central Amazonian forests that are prone to fire during severe ENSO events. Furthermore, the effects on animal abundance documented in this study should be

considered as conservative. As in logged forests (Johns 1997), many of the more mobile species recorded in burnt forest may have relied on the close proximity (< 5 km) of unburnt forest refuges for their survival, thus underestimating the detrimental consequences of fires in fragmented landscapes or areas far from primary forest. The scale of the effects attributable to fires may also have been influenced by the pre-burn history of hunting, which had already depressed the abundance of several large-bodied species that otherwise may have responded to fires. In addition, because of the largely impenetrable understorey, hunting pressure in burnt forest was much lower at the time of the study than in nearby unburnt forest. Finally, as data presented here are restricted to changes in abundance, they may overlook the true long-term effects of fires, as diet, territoriality, group size and other traits defining the feeding, ranging, reproductive and socio-ecology of frugivorous vertebrates can all be affected by changes in resource availability (Leighton and Leighton 1983; Terborgh 1983; Zhang 1995; O'Brien et al. 2003).

Potential changes in seed dispersal

Changes in large vertebrate abundance following forest disturbance can have severe effects on animal-mediated tree-seed dispersal and recruitment (Cordeiro and Howe 2001; Peres and Roosmalen 2002), especially in regions such as the neotropics, where density-dependent seed mortality is pervasive (Harms et al. 2000). Although fruit–frugivore interactions are typically diffuse (Janzen 1980; Sallabanks and Courtney 1993), declines in most large frugivorous primates could still have consequences for the dispersal of large seeded drupes that are beyond the handling capability of even the largest avian dispersers (Peres and Roosmalen 2002), while the decline of scatterhoarders such as agoutis could affect the dispersal of sclerocarpic fruits. However, the strength and outcome of changes in the disperser assemblage will depend on interactions with other density-dependent processes that can influence regeneration in tropical forests. For example, lower tree density in burnt forest should decrease inter-specific plant competition, perhaps reducing the need for long-distance seed dispersal during the regeneration phase. The reduction in fruiting tree density could also affect the probability of seed predation, and the regeneration of some species may be prevented if the seed rain is no longer sufficient to satiate seed predators (Curran et al. 1999).

However, the current phase of regeneration in the burnt forest plots was dominated by pioneer species, either dispersed abiotically or by the many small frugivorous birds found in the understorey of once-burnt forest 3 years after the fire (Barlow and Peres, 2004b). The rapid dispersal and large seed rain of these small-seeded species means they can be expected to dominate burnt forests for many years, even in the absence of additional large-scale disturbance (Slik et al. 2002). In the long term, the recovery of species typical of mature forests will depend on large mobile frugivores, which can serve an important

role as seed vectors as long as pioneer species in burnt forest are sufficiently attractive to them, or if disturbed forests retain at least some large fruiting trees or nest sites (Anggraini et al. 2000). However, even if primary forest is close enough to encourage seed dispersal, competition from aggressive annuals such as bamboo and other grasses can inhibit or prevent the growth and regeneration of forest species (Nepstad 1991), while large numbers of rodents (Doi 1988) could indicate higher rates of seed predation.

Conclusions

While single fires had a huge impact on the fruit resource base of once-burnt forest, this effect was greatly magnified in areas that succumbed to two fires within 10 years. Results from tree plots and fruit transects suggest that the mortality rate of fruit-bearing trees may be non-random at the family level, and that some important fruiting families may be especially vulnerable to thermal stress. There was also a suggestion that some families of tree had increased levels of fruit production in once-burnt forest, although any compensation was marginal compared to the loss of fruit production resulting from the high rates of tree mortality. The observed changes in the composition and abundance of fruit producing stems and the concurrent changes in habitat structure in burnt forest altered the abundance of many large-bodied vertebrate species, and extirpated many primary forest specialists in twice-burnt forest. Wildfires therefore represent a substantial threat to large vertebrates in Amazonian forests, especially as our results (from continuous forest within 5 km of unburned forest) may be conservative compared to those in fragmented landscapes or areas far removed from undisturbed forest.

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