Ecological responses to El Niño-induced surface fires in central Brazilian Amazonia: management implications for flammable tropical forests

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Over the past 20 years the combined effects of El Niño-induced droughts and land-use change have dramatically increased the frequency of fire in humid tropical forests. Despite the potential for rapid ecosystem alteration and the current prevalence of wildfire disturbance, the consequences of such fires for tropical forest biodiversity remain poorly understood. We provide a pan-tropical review of the current state of knowledge of these fires, and include data from a study in a seasonally dry *terra firme* forest of central Brazilian Amazonia. Overall, this study supports predictions that rates of tree mortality and changes in forest structure are strongly linked to burn severity. The potential consequences for biomass loss and carbon emissions are explored. Despite the paucity of data on faunal responses to tropical forest fires, some trends are becoming apparent; for example, large canopy frugivores and understorey insectivorous birds appear to be highly sensitive to changes in forest structure and composition during the first 3 years after fires. Finally, we appraise the management implications of fires and evaluate the viability of techniques and legislation that can be used to reduce forest flammability, prevent anthropogenic ignition sources from coming into contact with flammable forests and aid the post-fire recovery process.

Keywords: forest biomass; carbon; birds; large vertebrates; forest regeneration; phase-shift

1. INTRODUCTION

Tropical evergreen forests have long been considered virtually immune to sustained fires, largely because of excessively moist fuel conditions (Uhl 1998). Over the past two decades, however, this view has been gradually dispelled ever since large uncontrolled fires linked to severe ENSO events affected forests in East Kalimantan, Borneo, in 1982–1983 (Leighton & Wirawan 1986). More intensive and widespread recurrent fires also followed the 1997–1998 ENSO event with large-scale wildfires occurring throughout many seasonally dry forests of Southeast Asia (Guhardja *et al.* 2000), Mesoamerica (Anon. 1998) and Brazilian Amazonia (Nepstad *et al.* 1999; Peres 1999). As a result, tropical forest fires have been gradually attracting more attention from the science community (Wuethrich 2000). There is now a growing consensus that an unprecedented dynamic of frequent fire incursions and increasingly severe wildfires can become rapidly established in many previously unburned tropical forests (Cochrane *et al.* 1999; Goldammer 1999; Nepstad *et al.* 1999; Siegert *et al.* 2001).

Although fire is postulated to have played a role in shaping the present-day composition of some humid tropical forests (Charles-Dominique *et al.* 1998), their historical extent and severity remain largely unknown

(Kauffman & Uhl 1990). Furthermore, fires at any given site were unlikely to have occurred more than once or twice per millennium (Sanford *et al.* 1985; Turcq *et al.* 1998). By contrast, many present-day fire-prone forests exhibit fire-return rates of once or twice per decade (Cochrane & Laurance 2002), and the overwhelming majority of these fires are associated with anthropogenic influences. Human perturbation can aggravate the background rate of forest disturbance by either puncturing or opening up the canopy, thus greatly increasing fire susceptibility, which is largely a function of the relative humidity of the understorey (Kauffman & Uhl 1990; Cochrane & Schulze 1999; Cochrane *et al.* 1999). The intact canopy cover principally maintains high humidity by greatly reducing insolation and evaporation. Forests degraded by logging (Nepstad *et al.* 1999; Matricardi *et al.* 2001), edge-dependent effects of fragmentation (Laurance *et al.* 1997; Cochrane & Laurance 2002) and previous fires (Cochrane *et al.* 1999; Siegert *et al.* 2001) are then more likely to become vulnerable to recurrent fire disturbance. For example, alterations in forest structure caused by selective logging can result in far greater understorey fuel loads and a convective process that pumps moisture out of the understorey, leaving it warmer, drier and more susceptible to fire than primary forests (Uhl & Kauffman 1990; Holdsworth & Uhl 1997). This is reflected in the more frequent burns of logged forests (Uhl & Buschbacher 1985; Cochrane & Schulze 1999; Siegert *et al.* 2001).

This process also applies to forest edges in fragmented landscapes. Forest edges are associated with increased levels of solar radiation, wind disturbance and lowered

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367

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humidity (Kapos 1989), and canopy-gap dynamics can be altered up to 300 m into forest fragments. Edges therefore increase rates of tree mortality and leaf shedding during droughts (Laurance *et al.* 1997, 2000; Mesquita *et al.* 1999) creating a more open forest with larger amounts of fuel on the forest floor. Furthermore, a 'vegetation breeze' may act to pull moisture from the forest to the surrounding cleared land, with extensive clearings potentially resulting in large-scale forest desiccation (Laurance *et al.* 2002). Sustained wildfires, however, are not necessarily restricted to degraded forests and can affect vast tracts of largely undisturbed primary forests provided the appropriate edaphic conditions are combined with sufficiently long droughts (Peres 1999).

Exacerbating these conditions, at least 25–35% of the total rainfall in the Amazon is derived directly from evapotranspiration (Eltahir & Bras 1994), which in turn contributes more than 90% of the ambient water vapour (Moreira *et al.* 1997). Although small amounts of deforestation may initially lead to an increase in precipitation (because reflected heat promotes the formation of rain-producing clouds), reduced evapotranspiration caused by large-scale deforestation and forest degradation could lead to a sudden decrease in rainfall (Laurance *et al.* 2002), markedly increasing leaf-shedding and forest flammability. Furthermore, ENSO events may be becoming increasingly common as a result of global warming (Timmermann *et al.* 1999), in turn increasing the frequency of the severe droughts with which most fires are associated both historically (Sanford *et al.* 1985; Turcq *et al.* 1998) and in the past two decades (e.g. Woods 1989; Nepstad *et al.* 1999).

Despite the importance of wildfires as agents of change in humid tropical forests, relatively few studies have documented their consequences for plant and animal communities. We present an overview of the effects of wildfire on the structure and composition of tropical forests. We begin by reviewing the present state of knowledge concerning the effects of fires on tree mortality, forest structure and forest wildlife. We then present data from our field study in central Brazilian Amazonia and discuss the generality of these results. Finally, we assess the potential ecosystem changes and their implications for the management of fire-prone tropical forests.

(a) *Previous studies*

(i) *Forest structure*

Despite the importance of ground fires as catalytic agents of change in tropical forests, ecological studies documenting their consequences on forest structure and tree mortality have either been restricted to the seasonally dry forests near the phytogeographic limits of Amazonia (IBAMA 1998; Santos *et al.* 1998; Barbosa & Fearnside 1999; Pinard *et al.* 1999) or to heavily logged or fragmented forest landscapes in Malaysian Borneo (Woods 1989) and at the eastern extreme of the Brazilian Amazon (Holdsworth & Uhl 1997; Cochrane & Schulze 1999; Gerwing 2002). As a result of these studies, several hypotheses concerning the impact of fires on tree mortality have become established and can be summarized as follows.

(i) Tree mortality is a direct function of burn severity (Uhl & Kaufmann 1990; Pinard *et al.* 1999), and

more severe, recurrent fires kill a much greater proportion of standing stems than do initial low-intensity fires (Cochrane & Schulze 1999).

(ii) Following initially light burns, tree mortality is markedly size dependent, with smaller stems (i.e. 10–30 cm in diameter) having disproportionately higher levels of mortality than larger stems (Woods 1989; Holdsworth & Uhl 1997; Cochrane & Schulze 1999; Peres 1999; Pinard *et al.* 1999; Haugaasen *et al.* 2003). However, the survival advantage of large stems does not persist following more severe recurrent fires, where all stems appear to become equally vulnerable (Cochrane & Schulze 1999).

(iii) A temporal increase in tree mortality occurs over time following fire events, both within 1 year of fires (Holdsworth & Uhl 1997; Kinnaird & O'Brien 1998; Haugaasen *et al.* 2003), and from 1 to 2 years after fire disturbance (Cochrane *et al.* 1999).

We test these hypotheses in a region of central Brazilian Amazonia containing a large mosaic of unburned and burned forests that were widely affected by a large surface fire. In contrast to studies conducted elsewhere in Amazonia and Southeast Asia, these forests had never been heavily logged, and at the time of the study had not been fragmented by roads or cattle ranches. We examine in more detail the relationship between burn severity, tree mortality and changes in forest structure, focusing on the effects of single and recurrent fires, the vulnerability of different diameter size classes and temporal changes in mortality. Our results provide clear evidence that ENSO-induced fires can severely alter forest structure, composition and dynamics even in the absence of other disturbance agents such as selective logging or forest fragmentation.

(ii) *Faunal responses to wildfire*

Despite the paucity of information on the effects of fire on forest fauna, some generalizations can be made about the short-term responses to fire. It is hardly surprising that terrestrial vertebrates characterized by poor climbing abilities and low mobility should be affected by surface fires, and indeed reports of dead and injured animals in burned forests (including tortoises *Geochelone* spp. and agoutis *Dasyprocta* spp.) are not uncommon in the immediate aftermath of fires (Peres 1999; Peres *et al.* 2003). Many other arboreal vertebrate species appear to succumb to smoke asphyxiation, including several primate, sloth, porcupine, arboreal echimyid rodents and bird species (Mayer 1989; Peres 1999). Sub-lethal injuries of more mobile animals are also common, and local hunters have reported killing several terrestrial mammals (including armadillos *Dasypus* spp., brocket deer *Mazama* spp. and pacas *Agouti paca*) exhibiting fire-induced scars as much as 4 years after a large area of Amazonian forest succumbed to a recurrent fire (J. Barlow, unpublished data).

Animals surviving the fire and smoke essentially have two options: either to emigrate into nearby unburned areas (if available), or to remain within the burned forest matrix. Animals moving into unburned forest can expect to face interference competition through territorial aggression from conspecifics (e.g. Bierregaard & Lovejoy 1989), density-dependent reductions in fitness through

exploitative competition for food, mates or other resources, and could suffer disadvantages from their poor familiarity with the spatio-temporal distribution of resources, all of which can be aggravated by overcrowding. Only where population levels in adjacent unburned forest have been artificially reduced by game hunting is it possible to envisage a relaxation of density-dependent effects, although the life expectancy of emigrants may still be low if the local subsistence hunting pressure persists or increases, and is aggravated by collateral damage to food crops and other forest resources (Peres *et al.* 2003).

Individuals remaining in the burned forest face a different set of problems. Initially, large-bodied animals may be hunted relentlessly by rural peoples desperate to compensate for losses of food crops. This is exacerbated by the lack of cover resulting from the scorched understorey and loss of midstorey and canopy foliage (Haugaasen *et al.* 2003), and the increasing clumping of animals around remaining fruiting trees or patches of unburned forest (Lambert & Collar 2002). Reports of large numbers or entire groups of mid-sized to large-bodied diurnal primates (including *Cebus apella*, *Alouatta belzebul* and *Pongo pygmaeus*) being killed by hunters shortly after wildfires are not uncommon (Saleh 1997; J. Barlow, personal observation).

Animals that escape or are unaffected by hunting may face severe food shortages, as many canopy trees abort fruit crops and shed leaves following the traumatic heat stress (Peres 1999). In some cases, animals appear to be able to compensate by switching to alternative dietary items. For example, primates such as howler monkeys (C. Peres, personal observation) and orang-utans (Suzuki 1988) became increasingly folivorous, resorting to the post-fire regrowth of young leaves, while both pig-tailed macaques (*Macaca nemestrina*) and gibbons (*Hylobates muelleri*) took advantage of wood-boring insect outbreaks immediately after the 1982–1983 fires in Indonesia (Leighton 1983). However, dietary switching may not be an option for all species, and in the case of understorey birds, those with specialized dietary, foraging or habitat requirements are also the most likely to be extirpated from burned forest 1 year after fires (Barlow *et al.* 2002).

Information on the long-term effects of fires remains scarce, and comes mainly from studies conducted following the 1982–1983 fires in Southeast Asia (Berenstain 1986; Boer 1989). In general, large terrestrial browsers such as wild pigs (*Sus* spp.), banteng (*Bos javanicus*) and deer (*Cervus unicolor* and *Muntiacus muntjak*) appeared to be able to take advantage of newly available food sources, and recovered well from the fires (Wirawan 1985; Doi 1988; Mayer 1989). Rodents were also thought to have increased, leading to larger populations of small cats (Doi 1988). While mortality was initially high among reptiles (Leighton & Wirawan 1986), populations of most species were seen to recover over time (Boer 1989). However, other animals did not display the same resilience, and some nocturnal primates (western tarsiers *Tarsius bancanus* and slow loris *Nycticebus coucang*) and the Malayan sun bear (*Helarctos malayanus*) had been either locally extirpated or drastically reduced in numbers as of 1986 (Doi 1988; Boer 1989).

(b) *Wildfires in central Brazilian Amazonia*

We now summarize our findings on the effects of fires on understorey birds and large vertebrates in central Brazilian Amazonia. We draw comparisons from previous studies of fire disturbance in Southeast Asia, and assess the long-term threat of wildfires for tropical forest fauna.

(c) *Study area*

Our study was located in the Arapiuns and Maró river basins, western Pará, central Brazilian Amazonia (figure 1; 2°44′ S, 55°41′ W) from January 1998 to June 2002. These first- and second-order tributaries of the lower Tapajós river are fed by a clear-water catchment, draining from permeable and predominantly sandy soils that lie within a zone of high fire risk in Amazonian forests (Nepstad *et al.* 1999). Unlike other seasonal Amazonian forests that overlay clay soils (Uhl & Buschbacher 1985; Holdsworth & Uhl 1997), human-induced canopy disturbance resulting from selective logging does not appear to be a precondition for reaching the point of leaf-litter flammability in this region. Before the 1997–1998 fires, most of these forests had been logged for only three or four commercially valuable timber species, and this involved minimal damage to the residual stand, because round logs were typically processed *in situ* without machinery. The resulting products (dugout canoes and planks) were hauled from the felling site on hand carts, or less frequently by oxen. Because small-scale farming of cassava (the only other significant source of human-induced structural disturbance) was largely restricted to landholdings within 3 km of navigable rivers, the results reported here are from continuous expanses of forest, which lie adjacent to unburned forest areas used as controls. Although we do not have pre-burn data from this region, the assumption that these forests were similar in structure and composition before the fires was supported by interviews with local people, and by the similarity in the basal areas, stem densities and tree family abundances in unburned and once-burned plots sampled 1 year after the wildfire (Barlow *et al.* 2003*a*; Haugaasen *et al.* 2003).

2. METHODS

Habitat data were obtained from a total of 44 quarter-hectare (10 m × 250 m) forest plots from July 2000 to May 2001, including 16 plots placed in unburned, 22 in once-burned and 6 in twice-burned forest. The selection of plot location was aided by interviews with local people and by an initial survey of the area conducted immediately after the fires (Peres 1999). In common with other studies in Amazonia (e.g. Cochrane & Schulze 1999), placement of forest plots was occasionally restricted owing to the refusal of permission from some communities that were fearful of prosecution or suspicious of biopiracy. Although the origin of each plot was not selected randomly, the length of the plots ensured a strong random element in the forest type sampled and minimized any potential selection bias. Data on tree mortality and canopy cover were obtained from all 44 plots, whereas other habitat structure variables (including understorey openness, and woody and non-woody stem densities) were quantified only at a subset of 28 plots where understorey mist netting of diurnal birds was also conducted (figure 1). Thirteen of the habitat plots (six in unburned forest and seven in once-burned forest) had been previously sampled 1 year after the fire
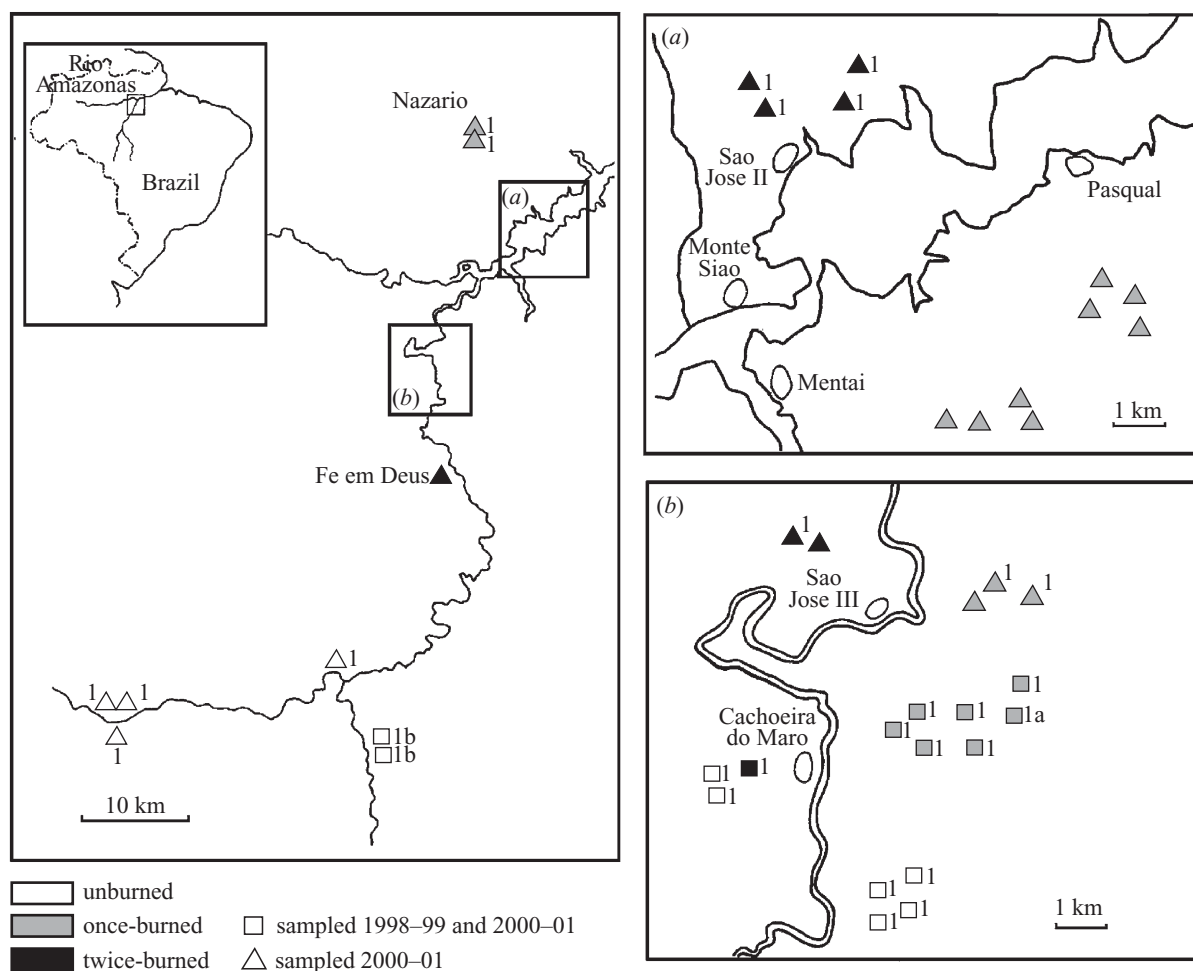
Figure 1. Map of study region, showing the location of all 44 0.25 ha forest plots. Plots marked with a 1 indicate those where avian mist netting was conducted. Although plot 1a was sampled in both periods, this was excluded from the analysis of temporal change because the exact location of the original plot could not be determined. Mist netting was conducted only in 1998–1999 in plots marked 1b.

(see Haugaasen *et al.* 2003), thus providing a temporal sequence of plant mortality (see Barlow *et al.* 2003*a*).

At each location a 0.25 ha plot (10 m × 250 m) was marked, and all trees and lianas 10 cm or more in diameter at breast height were measured (excluding those with more than half of their basal trunk outside the plot), and carefully inspected to determine their survival status (for details see Haugaasen *et al.* 2003). Diameter measurements were taken at breast height, or immediately above the tallest buttress whenever this exceeded breast height. Trees were measured with a diameter tape whenever possible, although visual estimates (from a single observer) were used in the very few cases when it was not possible to reach beyond or use sticks to hold the tape above the tallest buttress. The visible char height of the fires was noted on the trunk of all standing stems examined within burned-forest plots, and categorized as follows: 0 = no visible fire marks; 1 = burned at base to 30 cm, 2 = burned from 30 cm to breast height (1.3 m), and 3 = burned above breast height. The mean of these ranks was taken as an indicator of fire severity at each plot. All trees were identified at the level of genus or species using local names, and following Gentry (1993), Parrotta *et al.* (1995) and Ribeiro *et al.* (1999). Identifications based on vegetative plant parts were later verified by vouchers of fertile material collected over 14 consecutive months along 16 km of 1 m wide trails (Barlow 2003). The diameters of trees and lianas were converted into

above-ground dry biomass values using established equations (Putz 1983; Santos 1996). However, because only 64 woody lianas 10 cm or more in diameter (contributing only 0.36% of the total above-ground biomass) were measured, these were excluded from subsequent analyses.

Canopy cover was quantified with the use of a spherical densitometer at 24 evenly spaced points within each plot, with four readings taken per point (Lemmon 1957). Forest floor regeneration was examined at 24 locations along the 250 m transect, to the left of each point where a canopy reading was taken. All saplings and stems smaller than 10 cm in diameter and taller than 1 m in height were measured, and, whenever possible, identified to genus or species within a 10 m² (4 m × 2.5 m) quadrat. In some locations, bamboo culms were too numerous to measure or count, and their abundance was sub-sampled within a 1 m × 1 m quadrat representative of the larger 10 m² quadrat, and multiplied tenfold. Understorey vegetation openness was measured using a 2.5 m graduated pole held vertically 5 m from the transect, and examined at 12 m distance by an observer, also 5 m from the transect. Readings were taken according to the number of 10 cm pole sections (range of 0–25) that were clearly visible, and the procedure was repeated every 12 m on both sides of the transect ($n = 48$) with the positions corresponding to the location of individual mist nets.

Understorey mist-netting was conducted at 20 plots examined 1 year after fire (see Barlow *et al.* (2002) for site locations and mist-netting methodology) and in 28 of the 44 quarter-hectare plots examined 3 years after fire (Barlow & Peres 2004; figure 1). These 28 plots were placed in unburned ($n = 10$), once-burned ($n = 12$) and twice-burned ($n = 6$) forest. All birds were colour-banded to determine capture location and recaptures. In total, we obtained 5543 bird captures from 34 560 net-hours of sampling effort. Information on large-vertebrate abundance is derived from semi-structured interviews with local hunters (Peres *et al.* 2003), our observations spanning 20 field months and line-transect surveys. The surveys were conducted along four line transects of 4 km in length, located in unburned forest ($n = 2$), once-burned forest ($n = 1$) and twice-burned forest ($n = 1$). Each transect was walked twice every month for 14 months (February 2001–March 2002), resulting in 448 km of outward census effort (see Barlow 2003).

3. RESULTS

(a) *Tree mortality and forest structure*

Surface fires had decisive delayed effects on tree mortality in once-burned forest, and an additional 74 trees per hectare died between 1 and 3 years after fire. While a marked temporal increase in mortality was evident among smaller stems less than 30 cm in diameter, the greatest increase in mortality (relative to their original abundance) was found in the largest diameter class (50 cm or more in diameter; figure 2*a*). This delayed mortality reduced live tree biomass by an additional 107 Mg ha^{-1} in once-burned forest (Barlow *et al.* 2003*a*), substantially increasing committed carbon emissions under various scenarios of burn coverage in the Brazilian Amazon (figure 3).

Burn severity (mean char height) was a strong predictor of the number of standing live stems remaining (or tree mortality) in the 44 plots sampled 3 years after fire (figure 4). In once-burned plots, the live tree density (excluding regrowth of pioneers after the 1997–1998 fire) was, on average, only 58% of that found in the unburned forest. This was further reduced to just 26% in twice-burned plots. While trees of all size classes declined in abundance following recurrent fires (figure 2*b*), the sharpest decline relative to their initial abundance was in the largest size class (50 cm or more in diameter), resulting in a large decline in above-ground living biomass (figure 2*b*), and corresponding to large increases in committed carbon emissions (figure 3).

Changes in forest structure were strongly related to the live-tree density in each plot (figure 5), which was a good predictor of burn severity (figure 4). These structural responses to burn severity were mixed. The density of canopy gaps and the number of non-woody stems (such as bamboos and several Marantaceae species) increased exponentially (canopy gaps: $F_{1,42} = 123.0$, $r^2 = 0.75$, $p < 0.001$; non-woody stems: $F_{1,26} = 52.2$, $r^2 = 67$, $p < 0.001$), whereas understorey openness declined linearly ($F_{1,26} = 79.1$, $r^2 = 0.75$, $p < 0.001$) and the number of woody stems (less than 10 cm diameter) exhibited a unimodal response ($F_{2,25} = 9.5$, $r^2 = 0.43$, $p < 0.001$). As predicted, forest regeneration in once- and twice-burned plots was dominated by understorey and midstorey species of shrubs and treelets typical of highly disturbed forests and second growth (table 1). Most saplings recorded in the under-
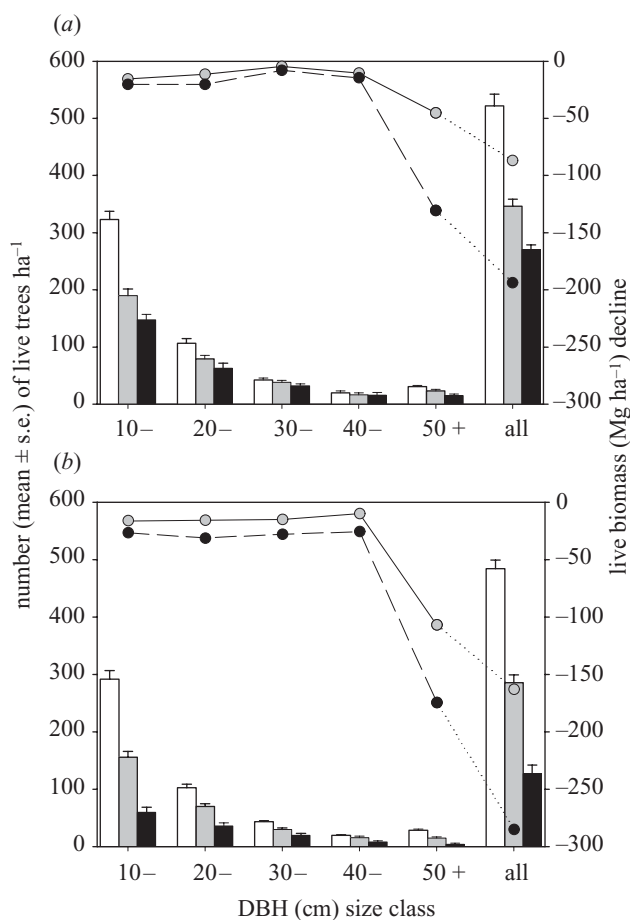

Figure 2. Mean number of live trees and above-ground biomass loss (relative to unburned primary forest) per hectare in different tree size classes showing (*a*) the temporal reponses to fires in primary forest plots (open bars; $n = 6$), and once-burned forest plots examined 1 year (grey bars; $n = 7$) and 3 years (solid bars; $n = 7$) after fire; and (*b*) the loss of live trees and biomass 3 years after fire, in primary forest (open bars; $n = 16$), once-burned forest (grey bars; $n = 22$) and twice-burned forest (solid bars; $n = 6$). Circle symbols indicate the mean decline in live biomass from unburned forest levels in each disturbance treatment.

storey of unburned forest plots were regenerating canopy tree species that produce fruits dispersed by large vertebrates, although *Rinorea* sp. (Violaceae), the most abundant understorey stem, is dispersed autochorously. By contrast, most saplings that dominated the forest understorey in once-burned forest plots were understorey and midstorey specialists, producing fruits dispersed by small avian frugivores, while abiotic modes of seed dispersal (i.e. autochory and anemochory) became increasingly prevalent in the regeneration phase of twice-burned forest plots (table 1).

(b) *Faunal responses*
(i) *Primates and other mammals*

Responses to fire after 1 year were mostly detrimental to vertebrate populations as animals either emigrated to escape the immediate food scarcity in the burned forest or succumbed to increased post-fire hunting pressure. Neither large frugivorous primates nor ungulates were recorded in the once-burned forest in five months of fieldwork conducted 1 year after the fires. Some recovery was
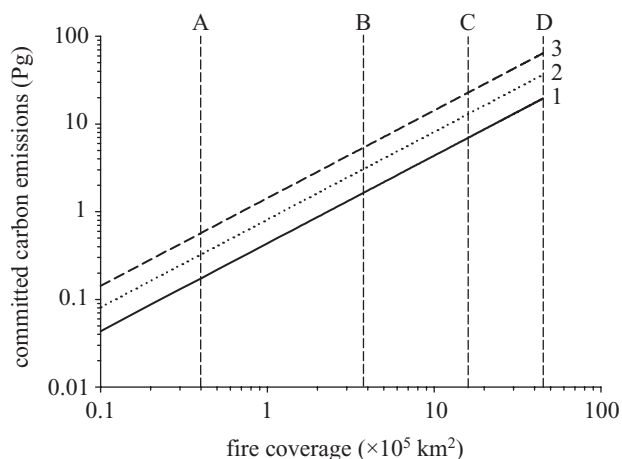
Figure 3. Predicted committed carbon emissions following three scenarios of fire-induced tree mortality and live biomass loss in our study area (1 = 1 year after fire in once-burned forest; 2 = 3 years after fire in once-burned forest; 3 = 3 years after fire in twice-burned forest) extrapolated for the entire forest cover within the Brazilian Amazon (indicated by line D). Lines A–C indicate scenarios of burn coverage in the Brazilian Amazon: A = the 30 000 km² of forest estimated to have burned in 1997–1998 (Diaz (and 6 others), unpublished manuscript); B = 270 000 km² of highly vulnerable forest in December 1998 (Nepstad *et al.* 1999); C = 1.5×10^6 km² of forest classed as either flammable or highly flammable in December 1998 (Nepstad *et al.* 2001).
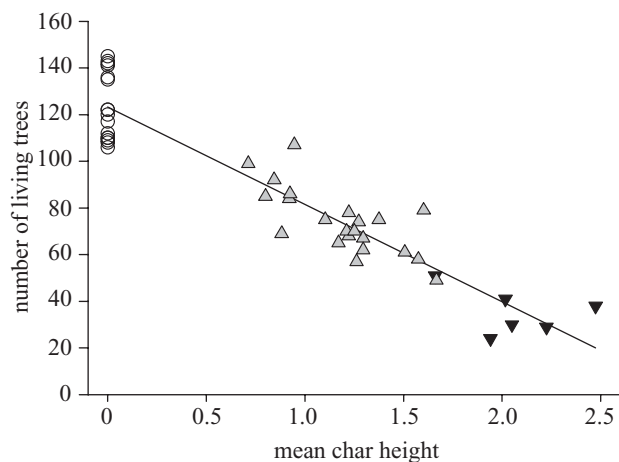

Figure 4. Relationship between burn severity (mean char height score) and the number of live trees in each quarter-hectare plot ($F_{1,42} = 313.2$, $r^2 = 0.88$, $p < 0.001$). Unburned, once-burned and twice-burned forests are indicated by open circles, grey triangles, and solid triangles, respectively.

evident 3 years after the fires, and although many species were too rare to be recorded in the 112 km of line-transect censuses conducted in once-burned forest, tracks around fruiting trees showed that tapir (*Tapirus terrestris*) and brocket deer (*Mazama americana* and *M. gouazoubira*) were at least occasional users of once-burned forest, while almost all primate species were recorded, albeit at very low densities. However, recurrent fires had far more pronounced effects, and resulted in the decline or extirpation of almost all forest species studied. Only small-bodied primates that are highly tolerant of second growth, such as marmosets *Callithrix humeralifera*, titi monkeys *Callicebus*

hoffmannsi and squirrel monkeys *Saimiri ustus*, were more abundant in twice-burned forest than unburned forest.

(ii) *Understorey and canopy birds*

Fires had substantial impacts on the understorey forest avifauna, and net-lines sampled 1 year after the fires in once-burned forest yielded fewer species and a lower abundance of birds than did those placed in unburned forest (Barlow *et al.* 2002). There was no change in the species richness or capture success in six unburned plots sampled 1 and 3 years after fires (mean ± s.e. species richness per net-line: 1998–1999 = 42.2 ± 2.6; 2000–2001 = 43.3 ± 4.7; mean ± s.e. capture success per net-line: 1998–1999 = 124.5 ± 7.0; 2000–2001 = 130.7 ± 16.2). By contrast, the same burned plots sampled 3 years after the fires ($n = 7$) displayed some signs of recovery in terms of bird species richness (mean ± s.e. species richness per net-line: 1 year after fire = 31.6 ± 2.7; 3 years after fire = 49.4 ± 2.4) and overall abundance (mean ± s.e. capture success per net-line: 1 year after fire = 73.1 ± 5.1; 3 years after fire = 168.0 ± 11.2). However, the avifaunal assemblage also became increasingly dissimilar to unburned forest over the same interval, and contained a higher abundance of species associated with second-growth habitats, such as the moustached wren (*Thryothorus genibarbis*) and the blackish antbird (*Cercomacra nigrescens*; Barlow 2003).

Species turnover and changes in the avifaunal assemblage 3 years after fire were strongly associated with changes in habitat structure such as canopy cover and understorey regeneration (Barlow & Peres 2004), which were in turn determined by local burn severity (figure 5). The average similarity (using the Bray–Curtis similarity measure) between net-lines in once-burned and unburned forest was merely 29%, compared with the mean background similarity of 54% between the 10 unburned plots. This decreased markedly in twice-burned forest to only 6%, and virtually no bird species were shared between the two extremes of the disturbance continuum. Foraging guilds were also severely affected by burn severity, although response types differed among guilds. Most insectivorous foraging guilds declined owing to fires, although arboreal-gleaning insectivores increased in abundance along the positive gradient of burn severity. All dead-leaf gleaning and ant-following birds were extirpated from twice-burned forest, while arboreal nectarivores, granivores and frugivores were most abundant in once-burned forest sampled 3 years after fire (table 3). Large canopy birds feeding partly or entirely on fruit were affected in a similar fashion to arboreal frugivorous mammals, with large toucans *Ramphastos* spp., pigeons *Columba* spp., red-throated caracaras *Daptrius americanus* and oropendulas *Psarocolius* and *Gymnostinops* spp. all declining appreciably after single and recurrent fires.

4. DISCUSSION

(a) *Effects on tree mortality and forest structure*

Levels of tree mortality in once-burned forest observed in this study (42%) are comparable with those in selectively logged forests in Paragominas and Tailândia, eastern Brazilian Amazonia (36–54%: Kaufmann 1991; 44%: Holdsworth & Uhl 1997; 38–66%: Cochrane *et al.* 1999;
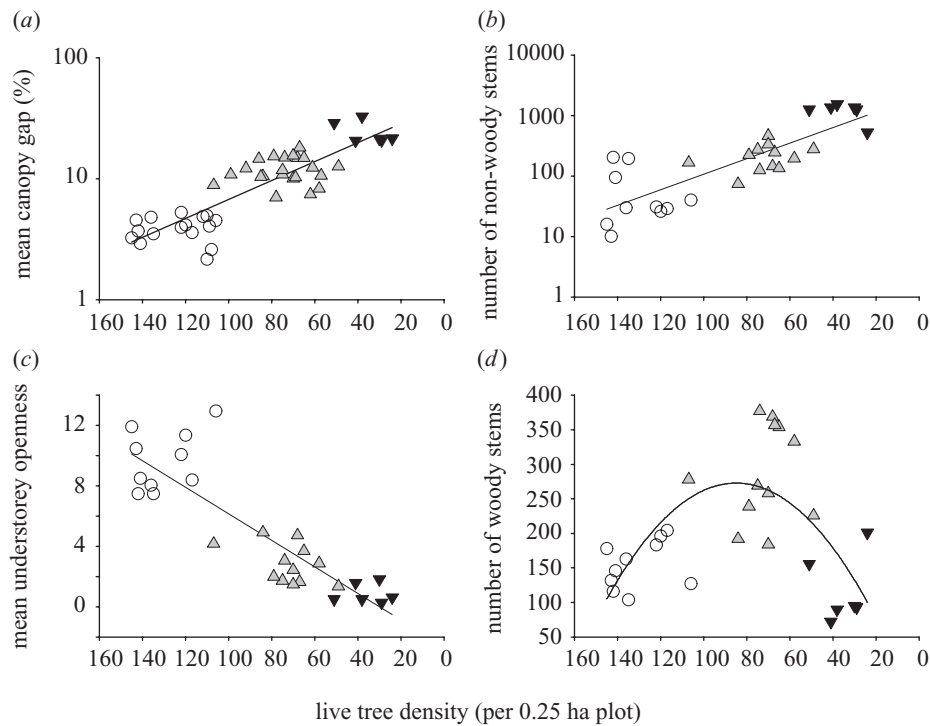
Figure 5. Changes in forest structure 3 years after fire disturbance in relation to local burn severity (here indexed as the number of live trees per plot). Unburned, once-burned and twice-burned forests are indicated by open circles, grey triangles and solid triangles, respectively. (*a*) $r^2 = 0.75$; (*b*) $r^2 = 0.67$; (*c*) $r^2 = 0.75$; (*d*) $r^2 = 0.43$.

Table 1. The six most abundant species of saplings (woody stems less than 10 cm in diameter and more than 1 m in height) in unburned, once-burned and twice-burned forest plots.

species	family	stems per 100 m^2	height[a]	dispersal agent[b]
unburned				
Rinorea sp.	Violaceae	6.4	US	autochorous
Protium and *Tetragastris* spp.	Burseraceae	1.8	CA	large birds/monkeys
Pouteria spp.	Sapotaceae	1.5	CA	large mammals
Talisia spp.	Sapindaceae	1.4	CA	primates
all genera	Lauraceae	1.0	CA	large birds
Sclerolobium spp.	Caesalpiniaceae	0.7	CA	anemochorous
once-burned				
Palicourea guianensis	Rubiaceae	10.1	US/MS	small birds
Cecropia and *Pourouma* spp.	Cecropiaceae	4.5	US/MS	birds
Aparisthmium cordatum	Euphorbiaceae	4.1	US	?
Miconia spp.	Melostomataceae	1.5	US/MS	small birds
Talisia spp.	Sapindaceae	1.4	CA	primates
Jacaranda copaia	Bignoniaceae	1.3	CA	anemochorous
twice-burned				
Aparisthmium cordatum	Euphorbiaceae	8.8	US/MS	?
unidentified sp.	Bombacaceae	1.5	US/MS	anemochorous
Palicourea guianensis	Rubiaceae	1.4	US/MS	small birds
Cecropia and *Pourouma* spp.	Cecropiaceae	0.8	US/MS	birds
Mabea spp.	Euphorbiaceae	0.8	US	autochorous
all genera	Annonaceae	0.7	CA	primates

[a] US, understorey; MS, midstorey; CA, canopy.
[b] Sourced from van Roosmalen (1985), Gentry (1993), Ribeiro *et al.* (1999) and authors' observations.

ca. 30%: Gerwing 2002), southern Nicaragua (44–54%: J. H. Vandermeer, personal communication) and Sabah, Malaysian Borneo (53%: Woods 1989), despite substantial differences in logging intensities and natural disturbance regimes. However, these levels of mortality are all considerably higher than those reported for drier forests

affected by surface fires near the southwestern and northern phytogeographic limits of Amazonia. For example, the mean rate of tree mortality induced by surface fires was 23% in a northern Bolivian forest (Pinard *et al.* 1999) and 8–16% in the northern Brazilian State of Roraima (IBAMA 1998; Santos *et al.* 1998; Barbosa & Fearnside

Table 2. Main responses of a central Amazonian avifauna to short-term (1 year after a single burn), medium-term (3 years after a single burn) and recurrent fires (examined 3 years after the most recent fire event).
(↔, no change detected; ↓ or ↑, slight decline or increase; ⇊ or ⇈, strong decline or increase; ⇊⇊, extremely rare or conspicuously absent from burned forest.)

foraging guild	short-term	medium-term	recurrent fires
understorey species			
dead-leaf gleaning insectivores	⇊⇊⇊	⇊⇊	⇊⇊⇊
ant-following insectivores	⇊⇊	⇊⇊	⇊⇊⇊
terrestrial-gleaning insectivores	⇊⇊	↓	↓
bark-searching insectivores[a]	↔	↔	↓
arboreal-gleaning insectivores	↔	↑	⇈
arboreal-sallying insectivores	⇊⇊	↓	⇊⇊
arboreal omnivore	⇊⇊	↔	↔
arboreal granivore	⇈	⇈	↔
arboreal nectarivore	↑	⇈	↔
arboreal frugivore	↔	⇈	↔
canopy species			
canopy frugivores	n.a.	↓	⇊⇊

[a] Feeding superficially.

1999) where large-scale fires in early 1998 were heavily publicized by the Brazilian and international media. Presumably, a recurrent fire regime over a much longer time-span in these regions (Sanford *et al.* 1985) has selected for more-resilient tree species with some fire-resistant traits. By contrast, few tree species in the central and eastern Brazilian Amazon are fire-adapted (Kauffman & Uhl 1990), and most are characterized by morphological traits such as thin bark and buttresses that have been associated with a high risk of fire-induced mortality (Uhl & Kauffman 1990; Pinard & Huffman 1997; Barlow *et al.* 2003b).

Overall, the generality of findings and predictions from other studies on the effects of wildfires in neotropical forests were supported here. Tree mortality was strongly related to burn severity (mean char height) at each forest plot (figure 4; cf. Uhl & Kaufmann 1990; Pinard & Huffman 1997), and recurrent fires had a much stronger effect than did single burns, with large-stemmed trees no longer holding a clear survival advantage detected after the initial fire (figure 2b; Cochrane & Schulze 1999). However, by examining the temporal sequence of mortality in once-burned forest up to 3 years after the initial fire, we found that the short-term survival advantage initially attributed to large trees following low-intensity fires (Holdsworth & Uhl 1997; Cochrane *et al.* 1999; Peres 1999; Haugaasen *et al.* 2003) may be simply an artefact of research methods, since large trees damaged by blazes appear to take longer to succumb to lethal fire stress (Barlow *et al.* 2003a). Large trees also suffer high mortality rates following recurrent fires (Cochrane *et al.* 1999; figure 2b), droughts (Leighton & Wirawan 1986; Swaine 1992; Condit *et al.* 1995), forest fragmentation and edge effects (Laurance *et al.* 1997, 2000), and, perhaps owing to greater hydraulic stress (Midgley 2003) or increased vulnerability to windthrow or pathogen attack, appear to be one of the most susceptible tree-size class to current patterns of forest disturbance.

This progressive increase in large-tree mortality suggests that previous estimates of forest biomass loss following low-intensity burns (e.g. Nepstad *et al.* 1999; Cochrane 2001a) could be conservative, as they do not include the

delayed mortality of large trees which account for much of the above-ground forest biomass (Clark & Clark 1996). The inclusion of large-tree mortality could double estimates of committed carbon emissions resulting from low-intensity ground fires during severe ENSO events (Barlow *et al.* 2003a). However, these estimates exclude the potential net losses from the mortality of below-ground biomass, or from soil carbon pools that, as yet, have not been quantified. Moreover, high levels of uncertainty still surround estimates of carbon loss from above-ground forest biomass (figure 3). Although they may increase further if tree mortality continues beyond 3 years after fires, or if high rates of tree damage are also considered (Laurance *et al.* 1998), applying an allometric model (Chambers *et al.* 2001) that accounts for the lower living biomass of senescing larger trees may reduce the estimates. Also, if other fire-prone forests tend to hold lower total biomass levels or suffer lower rates of tree mortality (e.g. Barbosa & Fearnside 1999) than the forests examined here, regional committed carbon emissions could be lower than we have projected.

Despite these uncertainties, the overriding conclusion is that wildfires in Brazilian Amazonia have the potential to contribute substantial amounts of CO_2 to the atmosphere (Nepstad *et al.* 1999; Barlow *et al.* 2003a), and have effects much greater than those resulting from other forms of forest degradation. For example, the 41–74% biomass lost 3 years after the fires in all once-burned and twice-burned forest plots is substantially higher than the 9% of biomass lost 10–17 years after fragmentation and edge creation (Laurance *et al.* 1997). Moreover, fires can counteract the potential carbon sink that is provided by tropical forests. Assuming a 0.71 Mg ha^{-1} yr^{-1} net uptake of carbon by tropical forests (Phillips *et al.* 1998), fire disturbance in a single hectare would offset the annual uptake of 230 ha of primary forest if the fires are of low intensity, and 401 ha if the forest burned for a second time. Extrapolating from these figures, a recurrent fire coverage of only 112 219 km^2 would offset the estimated sink from the entire Brazilian Amazon, while a recurrent fire regime

threatens 259 000 km² of forest in southeastern Amazonia alone (Cochrane 2001*a*).

Even under relatively conservative scenarios of potential fire coverage (e.g. scenario B, figure 3), low-intensity fires could contribute as much as 2.2 Pg of carbon to the atmosphere, increasing to 3.8 Pg following a subsequent second fire across the same area. These figures are comparable to the 0.8–2.6 Pg C emitted from peat and forest fires in Indonesia in 1997 (Page *et al.* 2002), and to the 1.7 Pg C estimated to result from tropical deforestation each year (Malhi *et al.* 2002). However, the annual rates of emissions following surface fires will depend on the rates of post-fire biomass decomposition minus forest regeneration, both of which remain unquantified.

While these results relate to the effects of fire, it should be noted that severe drought-induced mortality could also account for 12–28% of stems in Southeast Asian forests (Woods 1989; Sunarto 2000). However, in both of these studies the additional effects of fire killed many more stems (33–72%). Despite the potentially strong influence of drought, we attribute the elevated tree mortality in our plots to the direct effect of fire, as background rates of mortality induced by seasonal drought tend to be far lower in Amazonian and Mesoamerican forests (*ca.* 1–3% in Laurance *et al.* (2001*a*) and 2% in Condit *et al.* (1995), respectively), and because a significant temporal increase in post-drought mortality was not detected in our unburned control plots (Barlow *et al.* 2003*a*). Nevertheless, as ENSO-related droughts can markedly increase tree mortality and affect the recruitment rate of canopy tree species (Curran *et al.* 1999), their effects on forest dynamics can be substantial, and mortality induced from successive severe droughts could open up the forest canopy and increase the flammability of affected forests.

(b) *Impact on vertebrate populations*

Despite the paucity of studies documenting responses of tropical forest animal populations to wildfires, some patterns are beginning to emerge. First, it is evident that the short-term effects of fire are frequently exacerbated by hunting, both in Amazonia (Peres *et al.* 2003) and in several parts of Southeast Asia (Saleh 1997; C. P. Yeager, personal communication). Wherever wildfires are caused by slash-and-burn subsistence agriculture, this situation is unlikely to change as ignition sources are often generated by the same people who subsidize their protein intake through hunting.

In the medium-term, our findings suggest that the rapid regeneration of early pioneer trees in burned forest had the dual compensatory effects of discouraging hunting pressure (by reducing hunter access and visibility within the forest), and providing an alternative resource pulse to terrestrial browsers and grazers. The same regeneration pulse also produced many of the small fruits, seeds and flowers that can explain the increase in understorey birds consuming these resources (table 1). This might also lead to an increase in phytophagous understorey insects (Basset *et al.* 2001), which would account for the increased abundance of live-leaf gleaning insectivorous birds. However, while many terrestrial and understorey species may benefit from the vertical shift of primary productivity from the forest canopy to the understorey, canopy species (with the exception of second-growth specialists) were detrimentally

affected by the sharp decline in live-tree density. This is consistent with similar responses by primate species observed in a fire-disturbed forest in southern Sumatra (O'Brien *et al.* 2003). Not surprisingly, these declines were increasingly severe in twice-burned forest, where many primary forest specialists were extirpated, and most species that had initially benefited from or were resilient to single burns declined (table 2). Finally, most of the burned-forest plots and transects were in forest adjacent to unburned forest and many of the wide-ranging species could have subsidized their diets in unburned forest. These shifts in abundance should therefore be seen as conservative indicators of the detrimental effects of fire.

(c) *Assessing ecosystem change*

The consequences of fires in tropical forest ecosystems will eventually be determined by the extent of fire coverage, the fire-return intervals and the intrinsic tolerance of the fire-disturbed biota to extreme heat stress. As fires are historically rare in the Amazon (Sanford *et al.* 1985; Turcq *et al.* 1998), an increased fire-return rate can be expected to select against species with life-history and morphological traits that are poorly adapted to fire disturbance events. Even under a relatively optimistic scenario of fire-return intervals (such as the 100–150 years predicted for some undisturbed forest interiors (Cochrane & Laurance 2002)), the biota of fire-prone forests can be expected to become increasingly impoverished, and perhaps reminiscent of second-growth stands (Slik *et al.* 2002) or the semi-deciduous forests at the fringes of the humid tropics.

However, a chain of interacting ecological, social and economic factors (Cochrane *et al.* 1999; Nepstad *et al.* 1999, 2001) threatens to decrease fire-return intervals far beyond a level that even fire-adapted or pioneer species with fast life histories can survive. Forest recovery following single and recurrent fire regimes will be further aggravated by: (i) the widespread mortality of saplings, seedlings and the soil seed bank; (ii) inappropriate microclimate for shade-tolerant species in burned-forest; (iii) suppressed regeneration of shade-intolerant species resulting from the rapid proliferation of early pioneers; and (iv) extirpation or very low abundance of many avian and mammalian seed dispersers. Moreover, compared with unburned forest, the value of burned forests for local extractive communities becomes severely reduced in terms of timber and non-timber products (Peres *et al.* 2003) rendering them more likely to be converted to more profitable land uses. This is already occurring in the Tapajós-Arapiuns Extractive Reserve, where there has been an increasing trend towards large-scale investments in cash crops and agroforestry at the expense of natural forest cover (J. Barlow and C. Peres, personal observation).

Left unchecked, self-perpetuating fires can rapidly transform closed-canopy forest ecosystems into low-biomass open forests more reminiscent of scrub-savannahs. At present, twice and thrice-burned forests southeastern and central Brazilian Amazonia are already dominated by flammable grasses and forbs (Cochrane & Schulze 1999; figure 5), and are subjected to fire-return intervals of less than a decade (Cochrane & Laurance 2002; J. Barlow, personal observation). This transition represents an ecosystem phase-shift from high-phytomass *terra firme* forest to fire-dominated scrublands, which is

Table 3. Main responses of a central Amazonian mammal fauna to short-term (1 year after a single burn), medium-term (3 years after a single burn) and recurrent fires (examined 3 years after the most recent fire event).
(↔, no change detected; ↓ or ↑, slight decline or increase; ⇓ or ⇑, strong decline or increase; ⇓⇓⇓, extremely rare or conspicuously absent from forest type.)

foraging guild	mammalian taxa included	short-term	medium-term	recurrent fires
arboreal folivores	*Bradypus*, *Choloepus* and *Alouatta*	↓	↓	⇓
arboreal frugivores	*Cebus apella* and *Cebus albifrons*	↓	↓	⇓⇓⇓
small arboreal frugivores	*Callithrix*, *Callicebus* and *Saimiri*	↔	↑	⇑
arboreal frugivores/granivores	*Pithecia* and *Chiropotes*	↓	⇓	⇓⇓⇓
	sciurids	n.a.	↓	↓
terrestrial granivores/frugivores	*Tayassu* spp. *Dasyprocta agouti*	↓	↓	↓
terrestrial frugivores/browsers	*Mazama* spp., *Tapirus*, *Agouti paca*	↓	↓	↓
carnivores	*Felis*, *Eira*, *Nasua*	↓	↔	↔

unlikely to be reversed under current climatic (Timmermann *et al.* 1999) and socio-economic conditions. Ultimately, the availability of ignition sources in the dry season combined with flammable conditions and continuous fuel loads are all it requires to start a catastrophic wildfire. Even if these fires only occur once or twice per century, succession could be deflected (Mueller-Dombois & Goldammer 1990), and large areas of tropical forests transformed for the foreseeable future.

(d) Management implications for fire-prone forests

The management of fire-adapted ecosystems centres on costly fire suppression and the use of prescribed burns (Martell 2001), neither of which are suitable for fire-intolerant humid forests. Rather than reducing fuel loads, any prescribed burns would have the paradoxical effect of increasing fuel loads (Cochrane & Schulze 1998; Cochrane *et al.* 1999). Moreover, the suppression of large wildfires would be beyond the logistical and economic means of most tropical countries, while the effectiveness of fire-fighting techniques has yet to be validated even where equipment and technology are readily available (Minnich 2001; Johnson *et al.* 2001). The only realistic method of fire control in the humid tropics is to prevent their occurrence in the first place. We consider two strategies that can be used to control fire: reducing forest flammability and preventing fire from reaching flammable forests.

(e) Reducing forest flammability

In both temperate and tropical forests, fire risk is closely associated with fuel humidity (Holdsworth & Uhl 1997; Johnson *et al.* 2001) and fuel loads (Minnich 2001). Although even undisturbed continuous forests can be susceptible to fire during severe droughts (Peres 1999), these ENSO-related reductions in dry season precipitation are beyond our control. Management options must therefore concentrate on minimizing the lowered understorey humidity (Holdsworth & Uhl 1997) and increased understorey fuel loads (Uhl *et al.* 1991) attributable to anthropogenic forms of disturbance such as selective logging and forest fragmentation.

Substantial reductions in forest flammability can be gained through the adoption of RIL practices that reduce both canopy openness and fuel loads on the forest floor. Even where the adoption of these methods does not prevent the occurrence of fires, they will at least reduce fire severity, and hence their impacts on biodiversity (Barlow 2003), forest recovery times and the chances of a recurrent-burn regime from becoming established. However, despite the many economic and environmental benefits associated with RIL, it is rarely adopted in tropical forests where most logging companies focus on short-term profits (Putz *et al.* 2000). While financial incentives have been proposed to encourage the adoption of RIL (Putz *et al.* 2000), this would require a level of regulation and enforcement beyond that currently available or realistic in the present logging industry (Laurance & Fearnside 2002). Furthermore, *ca.* 80% of logging operations in lowland Amazonia are illegal (Laurance 1998), and many are followed by human invasions thereby bringing ignition sources into contact with the flammable forests (Laurance 2001).

Current patterns of frontier advance have resulted in landscapes characterized by small irregularly shaped forest patches that are juxtaposed with frequently burned pastures, and even the larger fragments suffer from high edge to interior ratios (Cochrane & Laurance 2002). These forest patches are therefore extremely vulnerable to fire (Cochrane 2001*a,b*; Laurance & Williamson 2001; Cochrane & Laurance 2002) and eventual ecological implosion (Gascon *et al.* 2000). Furthermore, small forest fragments are often subjected to persistent hunting pressure and thereby have limited value for wildlife conservation even if they can be protected from wildfires and logging (Peres 2001*a*). Therefore, although legislation requiring landholders to maintain 50–80% of forest within their properties has helped retain some forest cover, it has failed to maintain forests that are ecologically viable under the current fire regime. We recommend legislation changes to the focus of the current Brazilian Forest Code, so that the protection of large forest areas with low edge to forest interior ratios is encouraged rather than the creation of small vulnerable fragments. These areas should be located so as to buffer the agricultural frontier against farther expansion into previously undisturbed wildlands, while the relaxation of restrictions in economically marginalized regions could foster the intensification of agricultural production and revitalization of ageing frontiers, potentially reducing pressure on new developing frontiers.

(f) Preventing combustion of flammable forests

Preventing ignition sources from reaching fire-prone forests may be achieved using small and large firebreaks,

education schemes and legislation (e.g. PROARCO), financial incentives to encourage fire-sensitive forms of agriculture (Nepstad *et al.* 2001), and the creation of substantial networks of protected areas that can serve as firebreaks as well as political obstructions to haphazard frontier advance.

Firebreaks have been advocated to prevent flame contact with flammable forests. Proposed methods range between the removal of all fuel from 5 m strips around logged forests (Holdsworth & Uhl 1997) and the maintenance of extensive swathes of undisturbed primary forest between logged forests and agricultural areas, which could act as firebreaks through their intact canopies and low understorey fuel loads (Nepstad *et al.* 1996; Holdsworth & Uhl 1997). Neither method, however, is without practical complications. Cleared strips would be expensive, require frequent maintenance, and may not prevent the transmission of blazes through sparks or tree falls. Strips of primary forest would be susceptible to edge effects that increase flammability (e.g. Laurance & Williamson 2001), and over time could be gradually eroded by fire (Cochrane & Laurance 2002), eventually becoming fire vectors rather than firebreaks. Furthermore, it would be difficult to prevent the illegal logging of these strips where they are accessible by roads or rivers. However, despite these problems, firebreaks may be successful in buffering flammable forests, and finding low-maintenance fire-resistant buffers that are financially viable should be considered a major research goal over the next decade.

Because of the huge social and economic cost of fires for rural communities (M. C. V. Diaz, D. Nepstad, M. J. C. Mendonça, R. Seroa da Motta, A. Alencar, J. C. Gomes and R. A. Ortiz, unpublished manuscript; Peres *et al.* 2003), educational schemes such as PROARCO and Programa Emergêrcia Fogo, which inform Amazonian landholders how to minimize the risk of fires spreading into forest, are often well received in communities that have a history of fire in their region (M. Carnelutti, personal communication). Where implemented, simple measures such as the clearing of fuel at the edge of agricultural plots that will be burned, and the ban on intentional burns during the driest months of the year, have been effective in preventing fires from spreading into surrounding forests. One of the advantages of these schemes is that the causes of fires can be targeted in areas that are most at risk. However, although financial and custodial punishments for people infringing these rules provide an added incentive, their effectiveness is often undermined because of poor governance in transient frontier communities (Nepstad *et al.* 2001; J. Barlow, personal observation). Furthermore, our experience suggests that people are reluctant to invest time and energy into changing their traditional agricultural practices in areas where fires have yet to burn large forest areas (a common opinion being that fires are not a problem in that region). Because fires often spread from neighbouring landholdings (Nepstad *et al.* 2001; J. Barlow, personal observation), and can burn for tens of kilometres where forests are contiguous, people investing in fire prevention often fail to accrue the benefits (Nepstad *et al.* 2001). Finally, fire-prevention schemes are expensive to implement and enforce (the PROARCO 1998–1999 campaign required a $20 million loan from the

World Bank), and recent successes will not be sustained without substantial additional funding.

Some authors speculate that the risk of wildfires in Amazonian forests will be reduced as fire-sensitive investment in the land (e.g. fences and perennial crops) increases, and suggest the use of financial incentives to encourage this switch (Nepstad *et al.* 2001; Carvalho *et al.* 2002). This approach has a twofold effect. First, the use of perennial crops will reduce the need for fire. Second, fire-sensitive investment increases the cost of accidental fires for farmers, and therefore their motivation to reduce fire risks using firebreaks and the timing of controlled burns. However, while this approach may reduce reliance on fire in ageing frontiers that are already degraded and impoverished, it may not restrict the use of fire in developing frontiers where fire-based agricultural practices tend to predominate. Furthermore, increasing the financial gains from agriculture in tropical forests is a double-edged sword, which without appropriate regulation can further encourage frontier advance and lead to increased rates of forest clearance (Fearnside 1987; Brown 1998; Angelsen & Kaimowitz 1999).

The most biodiversity-sensitive method for preventing fire regimes from reaching their destructive potential is to discourage frontier advance (cf. Laurance & Fearnside 2002). Indeed, without restrictions on frontier advance other schemes may face failure because incentives to adopt them will be encouraged only when the resource capital (i.e. forests) becomes scarce (Boserup 1965; Nepstad *et al.* 2001). However, the Brazilian Amazon is currently witnessing the opposite trend with the advent of road paving and fluvial waterway schemes (Avança Brasil; Laurance *et al.* 2001*b*; Nepstad *et al.* 2001; Peres 2001*b*) and the expansion of the soybean industry into central Amazonia (Fearnside 2001). It has been suggested that these economic developments could be beneficial (Carvalho *et al.* 2001; Nepstad *et al.* 2002*a*), as they could form the foundation for improved governance and institutional capacity that is required for the successful implementation of all the previously discussed measures. However, the extent to which the resulting environmental degradation can be offset by more effective institutional capacity and governance is far from certain (see Laurance & Fearnside 2002; Nepstad *et al.* 2002*a,b*) and changes in frontier governance seem unlikely to occur.

5. CONCLUSIONS

Fires are a powerful and largely novel disturbance agent in humid tropical forests. Our results concur with previous findings on the responses of plant and animal communities to fire, though the temporal increase in deaths of large trees indicates that previous assessments of fire-induced tree mortality may be conservative. Left unchecked, fires threaten to degrade millions of hectares of forest, potentially altering the hydrological regime of the entire region, as well as threatening global climate processes through the release of millions of tonnes of greenhouse gases into the atmosphere. Although substantial economic, social and ecological benefits can be gained from preventing a transition from closed-canopy tropical forest to scrub savannahs (Barlow *et al.* 2002; Diaz (and 6 others), unpublished manuscript), at present there is a lack of

political will or consensus about how this could be achieved. For example, wildfires in fire-adapted North American forests receive far more media attention than do those in tropical forests because the political focus is on property damage rather than biodiversity, while the focus of the media that did cover the 1998 fires in Amazonia and Southeast Asia concentrated on the socio-economic costs such as human health hazards and closure of airports. Current policies aimed at maintaining forest cover in agricultural landholdings do little to prevent forest fragmentation and the creation of forest edges susceptible to wildfires, while the legislation and institutional capacity-building required to prevent a new wave of fires from following the recent increases in road paving and development in the Amazon (Nepstad *et al.* 2002*a*) are yet to be demonstrated (Laurance & Fearnside 2002). Ultimately, success in preventing wildfire regimes from reaching their potential levels of damage in humid tropical forests will depend not only upon the implementation and deployment of sensible measures aimed at reducing the incidence of fire, but also the sustained investment in institutional capability and governance required to enforce these measures.

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GLOSSARY

ENSO: El Niño–Southern Oscillation
RIL: reduced impact logging