

## Fire as a large-scale edge effect in Amazonian forests

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**ABSTRACT.** Amazonian forests are being rapidly cleared, and the remaining forest fragments appear unusually vulnerable to fire. This occurs because forest remnants have dry, fire-prone edges, are juxtaposed with frequently burned pastures, and are often degraded by selective logging, which increases forest desiccation and fuel loading. Here we demonstrate that in eastern Amazonia, fires are operating as a large-scale edge effect in the sense that most fires originate outside fragments and penetrate considerable distances into forest interiors. Multi-temporal analyses of satellite imagery from two frontier areas reveal that fire frequency over 12–14-y periods was substantially elevated within at least 2400 m of forest margins. Application of these data with a mathematical core-area model suggests that even large forest remnants (up to several hundred thousand ha in area) could be vulnerable to edge-related fires. The synergistic interactions of forest fragmentation, logging and human-ignited fires pose critical threats to Amazonian forests, particularly in more seasonal areas of the basin.

**KEY WORDS:** Amazon, Brazil, conservation, carbon emissions, deforestation, drought, fire, habitat fragmentation, logging, rain forest, remote sensing, tropical forest

### INTRODUCTION

The Amazon basin contains nearly 60% of the world's remaining tropical rain forest, and plays critical roles in maintaining biodiversity, regional hydrology and climate, and carbon storage (Fearnside 1999). It also has the world's highest absolute rate of forest destruction, averaging roughly 3–4 million ha y<sup>-1</sup> (INPE 2001, Whitmore 1997).

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The rapid pace of Amazon deforestation is causing widespread habitat fragmentation. By 1988, the area of forest in the Brazilian Amazon that was fragmented ( $< 100 \text{ km}^2$  in area) or vulnerable to edge effects ( $< 1 \text{ km}$  from clearings) was over 150% larger than the total area deforested (Skole & Tucker 1993). Because over 15% of the Brazilian Amazon has now been cleared (INPE 2001), the total area altered by deforestation, fragmentation and edge effects may comprise a third or more of the region today (Laurance 1998).

Habitat fragmentation affects the ecology of Amazonian forests in many ways, such as altering the diversity and composition of fragment biotas (Bierregaard *et al.* 1992, Lovejoy *et al.* 1986) and changing ecological processes such as pollination and nutrient cycling (Didham *et al.* 1996, Klein 1989). Recent evidence indicates that fragmentation also alters rain-forest dynamics, causing markedly elevated rates of tree mortality, damage and canopy-gap formation (Laurance *et al.* 1998a), apparently as a result of microclimatic changes (Kapos 1989), increased wind turbulence and proliferating lianas near fragment edges (Laurance *et al.* 2001b). These changes lead to a substantial loss of living biomass in fragments that may be a significant source of greenhouse gas emissions (Laurance *et al.* 1997, 1998b).

In addition to fragmentation, Amazonian forests are being degraded by various other activities, such as human-ignited fires, legal and illegal logging, gold mining and over-hunting (Fearnside 1990, Laurance *et al.* 2001a). These additional threats may interact additively or synergistically with fragmentation. An increasing body of evidence, for example, reveals that fragmentation increases the vulnerability of Amazonian forests to fire (Cochrane & Schulze 1999, Cochrane *et al.* 1999, Gascon *et al.* 2000, Kauffman & Uhl 1990, Nepstad *et al.* 1999). This occurs because fragments have relatively dry, fire-prone edges (Kapos 1989), are juxtaposed with frequently burned pastures and regrowth forests (Nepstad *et al.* 1996, Uhl & Kauffman 1990), and are often degraded by selective logging, which increases forest desiccation and fuel loading (Holdsworth & Uhl 1997, Uhl & Kauffman 1990).

While it is apparent that fragmented forests are vulnerable to fires, the spatial scale of this phenomenon has not yet been quantified. Most fires originate in surrounding pastures or regrowth and then burn into fragment interiors, and thus appear to be operating as a kind of edge effect. To date, edge effects in Amazonian forests, such as alterations in microclimate, forest dynamics and faunal communities, have been shown to penetrate from 10–400 m into fragment interiors (Bierregaard *et al.* 1992, Laurance *et al.*, in press, Lovejoy *et al.* 1986). Preliminary evidence, however, suggests that some edge-related changes in tropical forests could penetrate much further than this, perhaps as far as several km into fragment interiors (Curran *et al.* 1999, Laurance 2000).

Here we provide evidence that, in two relatively seasonal landscapes of the eastern Amazon, fire is operating as such a large-scale edge effect. Using a simple mathematical model, we demonstrate that even large forest fragments

and isolated nature reserves could be vulnerable to edge-related fires. We argue that, if fragmented, large expanses of Amazonian forests are likely to be destroyed or severely degraded by fire.

#### METHODS

##### *Dynamics of rain-forest fires*

Natural fires occur only rarely in undisturbed tropical rain forests (Goldammer 1990). However, colonists and ranchers use fires both to clear forests and maintain pastures, which often burn into adjoining forest blocks. These surface fires are deceptively unimpressive, creeping along the ground as a thin ribbon of flames burning through the leaf litter. Except for areas with unusual fuel structure, the fires reach only 10 cm in height (Cochrane *et al.* 1999).

Even during extreme droughts, rain forests maintain high humidity that makes combustion difficult. Many surface fires burn during the day, only to be extinguished when relative humidity increases in the evening. Such fires, however, can smoulder in old treefalls and standing dead trees for up to several weeks, until conditions are right for the fire to continue propagating through the leaf litter. Surface fires may cover as little as 150 m distance in a day (Cochrane & Schulze 1998) but are deadly to trees, because the slow propagation results in long residence times of the flames at the base of encountered trees. Most rain-forest trees have thin bark (typically < 1 cm thick; Uhl & Kauffman 1990) and the heat of even small fires girdles many trees, killing around 40% of all standing stems ( $\geq 10$  cm diameter at breast height (dbh); Cochrane & Schulze 1999).

An initial surface fire kills mostly smaller trees (< 40 cm dbh), with trees continuing to die for 2 y or more. The forest canopy becomes fragmented and the quantity of dead fuels increases as dead leaves and trees begin to fall. Soon, the forest is far more prone to subsequent fires, because the diminished canopy allows rapid drying and the dying trees provide large amounts of combustible fuel.

Burned forests commonly adjoin fire-maintained pastures and agricultural lands. While initial rain-forest fires may require an extensive drought, subsequent fires can occur after just a few weeks without rain (Cochrane & Schulze 1999). Forests that burn a second time fare much worse because the fires are far more intensive, overwhelming the defences of even larger, thicker-barked trees. Typically, second fires kill 40% of the standing trees in all size classes, comprising around 40% of the standing biomass (Cochrane *et al.* 1999).

Subsequent fires are even more likely and severe. During the first several fires, more fuels are created than destroyed, and a positive feedback results in which each fire becomes more probable and intensive. This process can eradicate trees from an area and result in extensive grass invasion. In the absence of seed sources for grassland or open-woodland species, anthropogenic savanna

(sometimes with certain palm species) will result. For regions with a pronounced dry season, this conversion of rain forest to savanna is likely to be irreversible (Cochrane *et al.* 1999).

#### *Study areas*

The two study areas, Tailândia (2470 km<sup>2</sup>) and Paragominas (1280 km<sup>2</sup>), are in the eastern Brazilian Amazon and have extensively fragmented forest cover. Both areas have similar evergreen terra-firme forests and pronounced dry seasons, with mean annual rainfall ranging between 1500–2000 mm (Cochrane *et al.* 1999, Kauffman *et al.* 1995). The terrain in both areas is quite flat and uniform, but is dissected by a number of streams and small rivers.

Tailândia is a new frontier where large-scale deforestation began in the early 1990s when a government-sponsored colonization project was initiated. As is typical, a ‘fish-bone’ pattern of deforestation quickly developed as colonists situated along parallel roads employed slash-and-burn farming (Figure 1). By 1997, 44% of the area’s forests had been destroyed. Paragominas is an older frontier where logging and cattle ranching predominate (Figure 1). Large-scale clearing began in the early 1960s with construction of the nearby Belém–Brasília Highway. By 1995, 64% of the area’s forests had been destroyed. Further information on these study areas is provided in Cochrane (2000).

#### *Core-area model*

We used a mathematical ‘core-area model’ to predict the areal extent of edge-related fires in forest fragments of varying sizes and shapes (Laurance & Yensen 1991). This model provides accurate (> 99%) predictions of the size of unaffected core-area for any fragment based on three parameters: fragment area, a fragment-shape index (*SI*), and the average distance (*d*) to which edge effects penetrate into fragment interiors. *SI* is derived by dividing the fragment’s perimeter-length by that of an equal-sized circle, and varies from 1.0 for perfect circles to 8 or higher for very irregularly shaped fragments. *SI* is calculated as  $SI = P / (2[TA^{0.5}])$ , where *P* is the perimeter-length of the fragment and *TA* is fragment area. The core area (*CA*) is given by  $CA = TA - \text{affected area } (AA)$ , where  $AA = 3.55 d SI (TA/10^4)^{0.5}$ . *AA* is overestimated for more-circular fragments and is therefore adjusted downward by  $AA_{adj} = (0.265 AA) / SI^{0.5}$  (see Laurance & Yensen 1991 for a detailed explanation of the model).

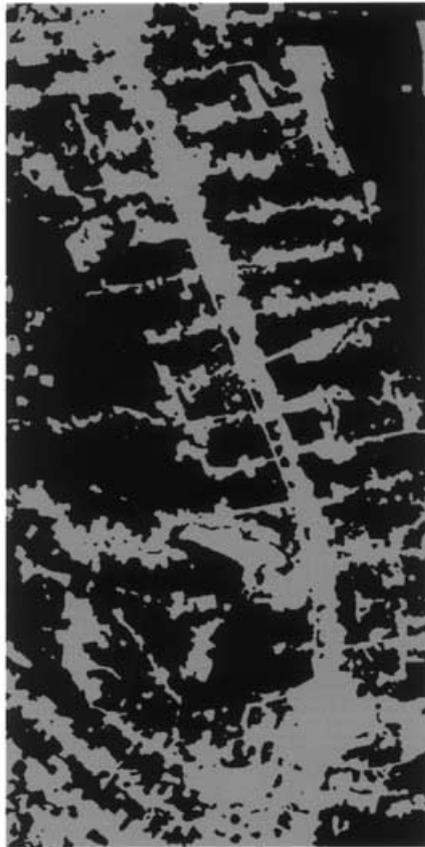
For both of our study areas, the total area and perimeter-length of all forest fragments of at least 0.1 ha were determined using georeferenced imagery from the Landsat Thematic Mapper (TM) satellite, at a 30-m spatial scale. Calculations were conducted using ArcInfo 8.0.1.

#### *Fire rotation-times*

The incidence of subcanopy-surface fires in the two study areas was assessed for periods of 12–14 y, from 1984 to the mid-late 1990s, using multi-temporal analyses of Landsat TM imagery, augmented with extensive ground-truthing



**Tailândia**



**Paragominas**

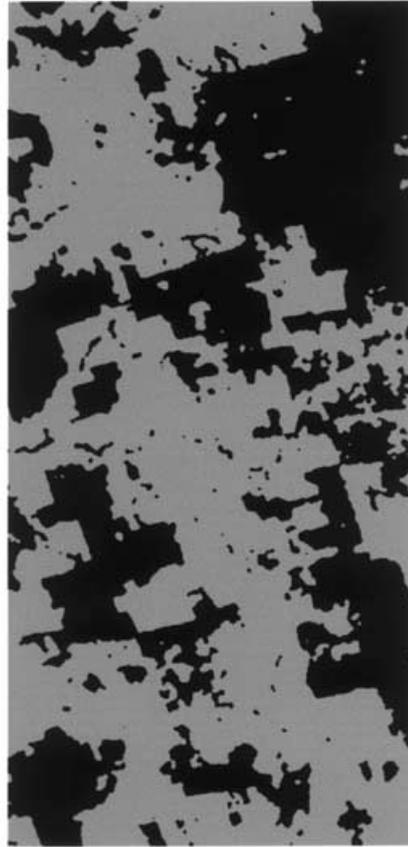


Figure 1. Map showing location of study areas. Below, portions of each study area in eastern Amazonia, showing the complex 'fish-bone' pattern of fragmentation arising from a forest-colonization project (Tailândia) and the somewhat less irregular fragmentation pattern caused by cattle ranching (Paragominas). Black areas are forest and grey areas are deforested. Each scene shows an area of about 600 km<sup>2</sup>.

and interviews of local residents (Cochrane *et al.* 1999). As is typical in the eastern Amazon, our study areas were affected by 2–3 droughts or rainfall deficits associated with periodic El Niño events (occurring in 1986 and 1991 at both sites, and in 1997 at Tailândia), during which forest burning increased markedly.

A sub-pixel linear spectral mixture-modelling technique (Cochrane & Souza 1998) was used to detect and classify forests that had been impacted by subcanopy surface fires in the Tailândia (1984, 1991, 1993, 1995, 1997) and Paragominas (1984, 1991, 1993, 1995) study areas. Specifically, fire-induced tree mortality opens the forest canopy, and even though the resulting gaps may be small they are sufficient to allow sunlight from more of the forest floor and woody vegetation to be reflected. These non-photosynthetic vegetation (NPV) reflections are a small fraction of the whole scene but the spectral signature of these substances is significantly higher in fire-damaged forests than in undamaged forests. Separation of satellite-imagery information into its fractional components (e.g. vegetation, shade, NPV) allows fire-damaged forests to be clearly distinguished for up to 2 y after a fire (in an earlier study, ground-truthing revealed that 93% of forests burned < 1 y previously and 71% of areas burned 1–2 y previously were correctly classified; Cochrane *et al.* 1999). A filtering technique was used to reduce the likelihood that logged forests could be misclassified as burned forests (Cochrane & Souza 1998).

In both study areas, fire rotation-times were calculated as a function of distance from forest edge (the fire rotation is the average number of years required to burn an area under consideration, with the understanding that some areas may not burn while others may burn more than once during a cycle; Van Wagner 1978). For each year of the study, all forest was mapped using classified images at a spatial scale of 30-m pixels. The area of forest in each edge-distance category (e.g. 0–30 m, 30–60 m, 60–90 m, etc.) was then calculated, using ArcInfo 8.0.1. Using the mixture-modelling technique described above, the distribution of surface fires was also mapped, and the proportion of pixels that burned in each edge-distance category was calculated. Data for all years of the study were then combined to yield an average proportion of burned pixels for each edge-distance category. The fire rotation-time was simply the inverse of this proportion (for example, if an average of 5% of all pixels at 0–30 m from the edge burned each year, then the fire rotation-time would be  $1/0.05 = 20$  y).

The distance ( $d$ ) to which fire rotation-times near forest edges deviated from those in forest interiors was estimated as follows: the 95% data distribution (mean  $\pm$  1.96 standard deviations) was calculated for fire rotation-times in forest interiors (defined by visual inspection as being over 2.5 km from the nearest edge); and the point at which the observed curve of fire rotation-times fell below this range was defined as  $d$ . The 95% data distribution is an appropriate measure of variability because fire rotation-times in forest interiors (at

Tailândia only; see below) did not deviate significantly from normality (Wilk-Shapiro test,  $P > 0.50$ ).

## RESULTS

### *Fragment characteristics*

We identified a total of 722 forest fragments in our two study areas, with individual fragments ranging from 0.1 ha to over 57 000 ha in area (Table 1). Small ( $< 100$  ha) forest patches were abundant, accounting for 91–93% of all fragments in each study area, but supported only a small proportion ( $< 4.5\%$ ) of the remaining forest cover at each site.

When shape index ( $SI$ ) values were plotted against fragment area, two trends emerged. First, there was a positive relationship between  $SI$  and area (Figure 2), because larger fragments tended to be more irregularly shaped than smaller fragments ( $r_s > 0.74$ ,  $P < 0.00001$  in both areas; Spearman rank correlations). This pattern resulted in part from fractal effects (because irregularities in the margins of small fragments tended to be smoothed over using 30-m pixels, thereby causing  $SI$  values of smaller fragments to be underestimated relative to those of larger fragments; cf. Li & Reynolds 1994). It does, nevertheless, reflect a tendency for most large fragments to be very irregularly shaped at a spatial scale that is relevant to edge effects in this system. Second, fragments in Tailândia were often more irregularly shaped than those in Paragominas (Table 1, Figure 2), reflecting the complex patterns of forest fragmentation caused by government-sponsored colonization projects in the Amazon.

### *Core-area model*

For Tailândia, fire rotation-times declined sharply near edges, and were found to deviate from those in forest interiors at a distance of up to 2.35 km from the forest edge (Figure 3). The core-area model for Tailândia was generated for fragments using shape indices of 2.0, 4.0 and 6.0. This range of values is realistic but slightly conservative; mean  $SI$  values for Tailândia ranged from 2.9 to 7.1 (Table 1), indicating that many fragments there were very irregularly

Table 1. Description of forest fragments in two study areas in the eastern Amazon. Tailândia (2470 km<sup>2</sup>) and Paragominas (1280 km<sup>2</sup>) had 419 and 303 fragments, respectively.

Fragment size-category (ha)	Per cent of fragments		Per cent of forest area		Mean fragment shape	
	Tailândia	Paragominas	Tailândia	Paragominas	Tailândia	Paragominas
<1	23.1	27.0	0.1	0.1	1.30	1.29
1–10	50.2	44.4	1.1	0.4	1.42	1.42
10–100	17.5	22.0	3.2	1.6	1.79	1.79
100–1000	6.9	5.5	14.8	5.6	2.33	2.94
1000–10 000	1.7	0.2	35.2	0.9	3.97	3.88
10 000–100 000	0.7	1.0	45.7	91.5	4.16	7.14

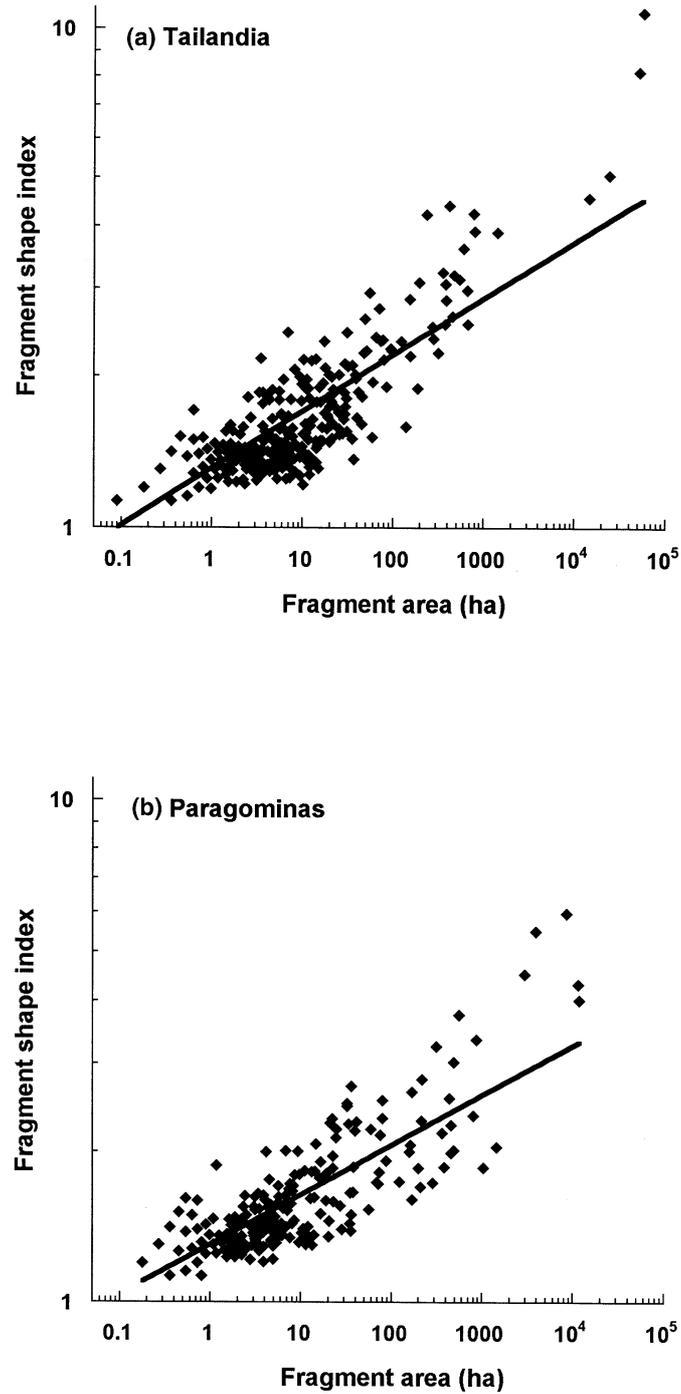


Figure 2. Relationship between fragment area and shape index (*SI*) for study areas at Paragominas and Tailândia in the eastern Amazon. Although *SI* values were somewhat underestimated in small fragments (because of fractal effects), this analysis reveals that most large fragments were very irregularly shaped at a spatial scale that is relevant to edge effects in this system.

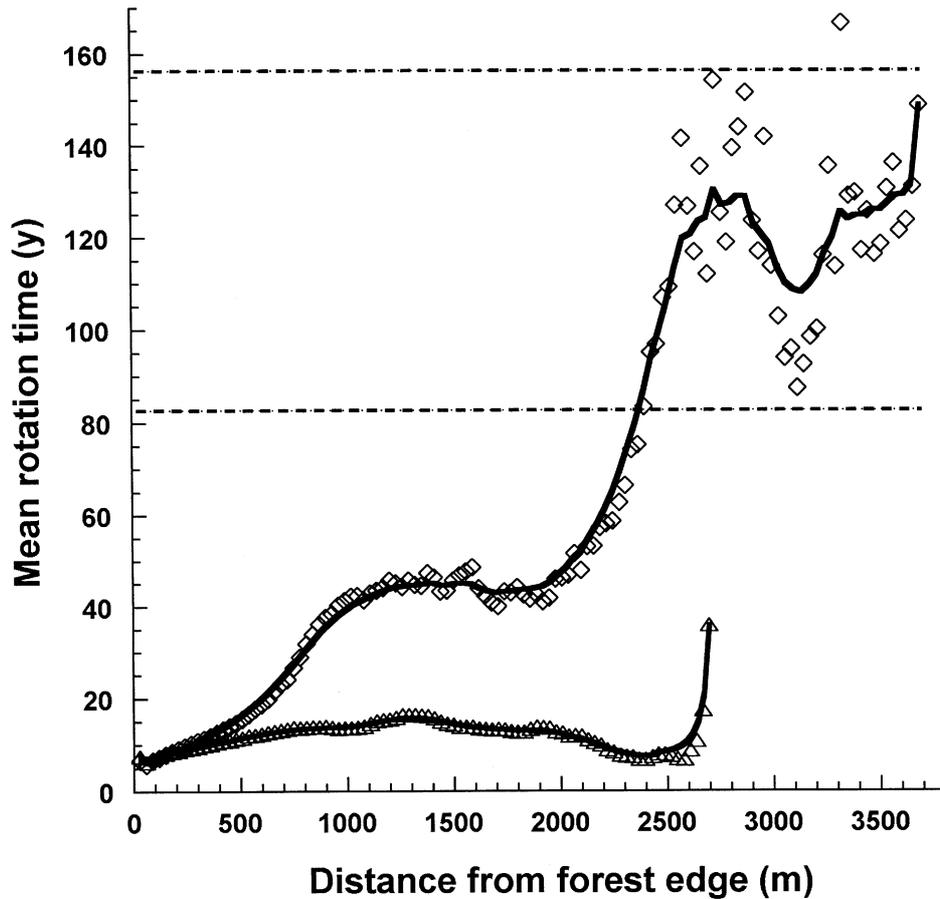


Figure 3. Fire rotation-times as a function of distance from forest edge for Tailândia (diamonds) and Paragominas (triangles). The curves were fitted with a smoothing function. Dotted lines show the 95% range of variation (mean  $\pm$  1.96 standard deviations) for forest interiors at Tailândia (more than 2500 m from edge).

shaped. The core-area model (Figure 4) suggests that fire regimes in even large fragments are being substantially altered. A fragment with an *SI* of 2.0, for example, would need to be about 90 000 ha in area to ensure that half of its total area will be unaffected by edge-related fires. If the fragment were more irregularly shaped (*SI* = 6.0), it would need to be about ten times larger (890 000 ha) to retain half of its total area in natural condition.

Fragments in Paragominas were generally less irregularly shaped than those at Tailândia, with mean *SI* values ranging from 2.3 to 4.3 (Table 1). The fragments in this older frontier, however, were often smaller, and the effects of fires even more devastating, than was observed at Tailândia. No forest at Paragominas was further than 2.7 km from the nearest edge, and even at this distance, predicted fire rotations were much shorter than those observed in forest interiors in Tailândia (Figure 3). Intact forest interiors have apparently

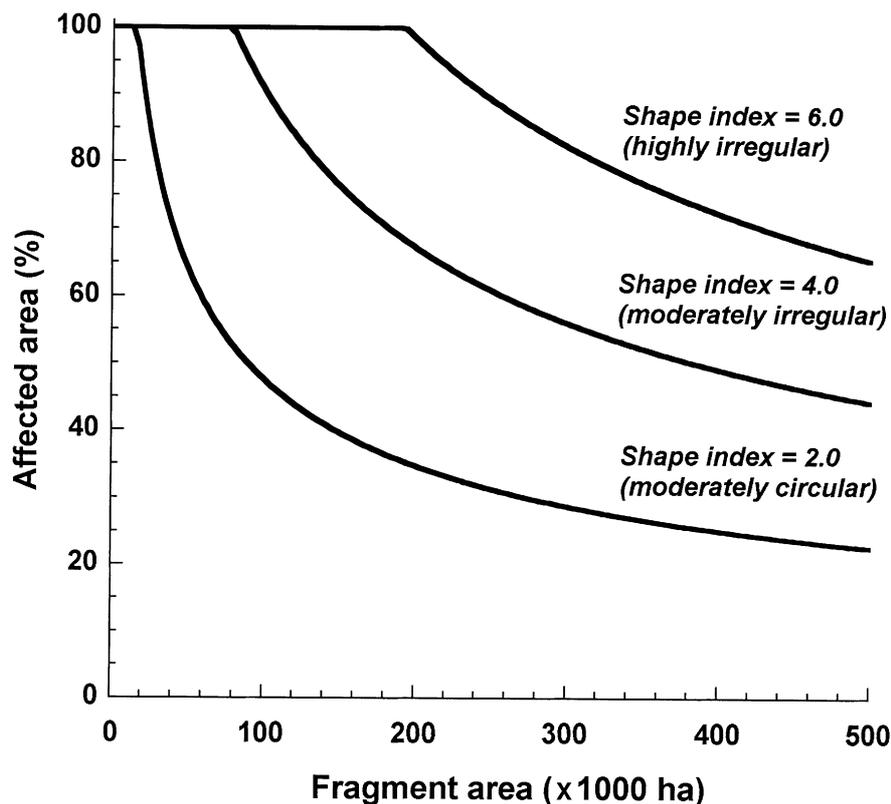


Figure 4. A core-area model showing the predicted impacts of edge-related fires on fragmented rain forests in Tailândia, Brazil.

vanished from the Paragominas area, and as a result it was not possible to estimate  $d$  and generate a core-area model.

#### DISCUSSION

##### *Generality and limitations of findings*

Our modelling results suggest that habitat fragmentation dramatically increases the vulnerability of rain forests in eastern Amazonia to anthropogenic fires, and that such fires are operating as an edge effect over surprisingly large spatial scales. Are our findings typical? Both of our study areas are experiencing intensive exploitation; the Paragominas forests, in particular, have been severely degraded over the past several decades. Nevertheless, the spatial patterns of forest fragmentation at our two sites are representative of those caused by ranching and large-scale forest-colonization projects, the two most prevalent land uses in the Amazon today. In addition, both of our study areas occur in relatively seasonal areas of the basin. However, about half of the closed-canopy forests in Brazilian Amazonia experience comparably strong dry seasons, especially in the eastern, southern and north-central areas of the basin (Nepstad *et*

*al.* 1994, 1999), and thus could be similarly susceptible to fire when fragmented. Analyses of recent Landsat TM imagery suggest that at least 45 000 000 ha of forest in Brazilian Amazonia (over 13% of the total remaining forest area) are currently vulnerable to edge-related fires (Cochrane 2001).

Our study was only 12–14 y in duration – the period over which satellite imagery of sufficient resolution was available – and our results might be biased if weather conditions during this interval were unusually dry. During the study there were moderate El Niño droughts in 1986 and 1991 at both sites, and a strong drought in 1997 at Tailândia, and most forest burning occurred during these drier years (Cochrane 2000, Cochrane *et al.* 1999). Nevertheless, over the last century there have been 23 El Niño events in the Amazon (Suplee 1999), and the 1997 drought was comparable to other strong droughts, such as that in 1983. Thus, droughts or rainfall deficits appear to be relatively common occurrences in the eastern Amazon, and the overall weather patterns during our study did not seem unusual.

Previous studies suggest that, under natural conditions, major fires are rare in Amazonian terra-firme forests, perhaps occurring only once or twice per millennium on average (Meggers 1994, Piperno & Becker 1996, Saldarriaga & West 1986, Sanford *et al.* 1985). At Tailândia, however, fires in intact forest interiors appeared to occur more frequently than this, with observed burns implying fire return-intervals of 100–150 y (Figure 3). Although this pattern could have resulted from the relatively seasonal nature of the Tailândia climate, we believe a more plausible explanation is that loggers or hunters occasionally ignited fires in forest interiors. Because our study was relatively short-term, even a few small fires in forest interiors could decrease the inferred fire rotation-time substantially. If so, then our analysis of edge-related fire frequency might be conservative, tending to underestimate the distance to which altered fire regimes penetrate into forest interiors.

It must be emphasized that our core-area model (Figure 4) predicts only the effects of habitat fragmentation on fire frequency, and does not consider the influence of other factors, such as temporal variability in weather and local topography. Clearly, forest fires vary in severity and frequency among years; the estimated fire rotation-times used in our model (Figure 3) are 12–14-y averages, and may not be typical of any single year. Topography also influences fire behaviour; trees along rivers and swamps, for example, are less likely to burn than those in upland areas (e.g. Kellman & Meave 1997). Nevertheless, fire frequency in our study areas was increased so radically near fragment edges that local topographic effects were largely obscured. The high incidence of logging in fragmented Amazonian landscapes (e.g. Nepstad *et al.* 1999) will further increase the vulnerability of forest remnants to fire.

#### *Implications for forest management*

Until the past few decades, major fires have been very rare in Amazonian forests. As a result, few rain-forest species are adapted for fire (Goldammer

1990, Kauffman & Uhl 1990) and even low-intensity surface fires that usually originate in adjoining burned pastures kill many rain-forest trees (Cochrane & Schulze 1999, Kauffman 1991). Such surface fires increase fine litter, wood debris and canopy openness, making forests highly vulnerable to intensive wild-fires in the future. In recurring fires, up to 98% of all trees become susceptible to fire-induced mortality (Cochrane *et al.* 1999).

An earlier study in Australia suggested that fire return-intervals of less than 90 y might eliminate rain-forest tree species, while intervals of less than 20 y could eradicate all but short-lived pioneer trees (Jackson 1968). Our analyses suggest that forests within 2.35 km of edges at Tailândia, and all remaining forests in Paragominas, had average fire return-intervals less than that evidently required to maintain rain-forest trees. Of equal concern is that fire return-intervals were less than 20 y – the threshold at which non-pioneer trees may be largely eradicated – within 600–700 m of edges at Tailândia and at least 2500 m of edges at Paragominas (Figure 3). These patterns suggest that rain forests in both study areas will be largely replaced over time by anthropogenic savannas and scrubby regrowth. Fire-adapted trees (e.g. *Byrsonima* spp., *Curatella* spp., certain palms) are unlikely to colonize these areas because there are no natural savannas or open woodlands nearby. The predicted deforestation process may be reinforced not only by the tendency for once-burned forest to become far more vulnerable to subsequent fires (Cochrane & Schulze 1999, Cochrane *et al.* 1999), but also by reductions in rainfall caused by increasing deforestation (Lean & Warrilow 1989, Shukla *et al.* 1990) and by the moisture-trapping effects of smoke caused by extensive forest and pasture fires (Rosenfeld 1999).

Because fragmentation drastically increased fire incidence, it appears likely that the margins of many forest fragments will recede over time, leading to a progressive ‘implosion’ of the fragments. Gascon *et al.* (2000) suggested that Amazonian fragments of less than 5000 ha will be susceptible to such effects, but our results imply that much larger fragments (up to several hundred thousand ha) could also be vulnerable to edge-related fires. An important factor in this regard is that prevailing land-uses in the Amazon, such as forest-colonization projects, produce forest remnants that are highly irregular in shape and thus vulnerable to edge-related fires and other external disturbances (Bierregaard *et al.* 1992, Laurance *et al.*, in press, Lovejoy *et al.* 1986). Because forest margins will tend to erode over time, the predictions of our static core-area model may be conservative, and a dynamic modelling approach would be useful for predicting longer-term interactions of fragmentation and fire.

A key implication of our study (see Figure 4) is that even the largest Amazonian nature reserves, if isolated by swaths of deforested land, may be seriously degraded by fires. This is especially likely to occur in the extensive areas of the basin with pronounced dry seasons. In such areas, nature reserves are likely to require deep buffers (> 3 km wide) of intact forest to ensure they are not

chronically degraded by fires and other edge-related phenomena. Adequate staffing and protection of reserves is also critical; a recent analysis of 86 federal parks and protected areas in Brazil found that 43% were at high to extreme risk because of illegal logging, deforestation, colonization, hunting, isolation of the reserve from other forest areas, and additional forms of encroachment. More than half of all reserves (54.6%) were judged to have nearly non-existent management (Ferreira *et al.* 1999).

Future changes in climate could make the Amazon even more vulnerable to fire. Some leading global-circulation models suggest that global warming may increase the frequency of El Niños (Timmerman *et al.* 1999) and warm-weather events (Mahlman 1997). Such changes, in concert with rapid forest fragmentation and logging, have the potential to accelerate losses of rain forest across large expanses of the Amazon basin.

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#### LITERATURE CITED

- BIERREGAARD, R. O., LOVEJOY, T. E., KAPO, V., DOS SANTOS, A. A. & HUTCHINGS, R. W. 1992. The biological dynamics of tropical rain forest fragments. *Bioscience* 42:859–866.
- COCHRANE, M. A. 2000. Forest fire, deforestation and landcover change in the Brazilian Amazon. Pp. 170–176 in Neuenschwander, L. F., Ryan, K. C., Gollberg, G. E. & Greer, J. D. (eds). *Crossing the millennium: integrating spatial technologies and ecological principles for a new age in fire management*. University of Idaho, Moscow.
- COCHRANE, M. A. 2001. In the line of fire: Understanding the impacts of tropical forest fires. *Environment* 43:28–38.
- COCHRANE, M. A. & SCHULZE, M. D. 1998. Forest fires in the Brazilian Amazon. *Conservation Biology* 12:948–950.
- COCHRANE, M. A. & SCHULZE, M. D. 1999. Fire as a recurrent event in tropical forests of the eastern Amazon: effects on forest structure, biomass, and species composition. *Biotropica* 31:2–16.
- COCHRANE, M. A. & SOUZA, C. M. 1998. Linear mixture model classification of burned forests in the eastern Amazon. *International Journal of Remote Sensing* 19:3433–3440.
- COCHRANE, M. A., ALENCAR, A., SCHULZE, M. D., SOUZA, C. M., NEPSTAD, D. C., LEFEBVRE, P. & DAVIDSON, E. 1999. Positive feedbacks in the fire dynamics of closed canopy tropical forests. *Science* 284:1832–1835.
- CURRAN, L. M., CANIAGO, I., PAOLI, G., ASTIANI, D., KUSNETI, M., LEIGHTON, M., NIRARITA, C. & HAERUMAN, H. 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* 286:2184–2188.
- DIDHAM, R. K., GHAZOUL, J., STORK, N. E. & DAVIS, A. J. 1996. Insects in fragmented forests: a functional approach. *Trends in Ecology and Evolution* 11:255–260.
- FEARNSIDE, P. M. 1990. Environmental destruction in the Amazon. Pp. 179–225 in Goodman, D. & Hall, A. (eds). *The future of Amazonia: destruction or sustainable development?* MacMillan, London.
- FEARNSIDE, P. M. 1999. Biodiversity as an environmental service in Brazil's Amazonian forests: risks, value and conservation. *Environmental Conservation* 26:305–321.

- FERREIRA, L. V., DE SÁ, R. M. L., BUSCHBACHER, R., BATMANIAN, G., BENSURAN, B. R. & COSTA, K. L. 1999. *Áreas protegidas ou espaços ameaçados?* World Wide Fund for Nature, Brasília.
- GASCON, C., WILLIAMSON, G. B. & DA FONSECA, G. A. B. 2000. Receding edges and vanishing reserves. *Science* 288:1356–1358.
- GOLDAMMER, J. G. (ed). 1990. *Fire in the tropical biota*. Springer-Verlag, New York.
- HOLDSWORTH, A. R. & UHL, C. 1997. Fire in the eastern Amazonian logged rain forest and the potential for fire reduction. *Ecological Applications* 7:713–725.
- INPE 2001. *Deforestation estimates in the Brazilian Amazon, 2000*. National Institute for Space Research (INPE), São Jose dos Campos, Brazil.
- JACKSON, W. D. 1968. Fire, air, water and earth: an elemental ecology of Tasmania. *Proceedings of the Ecological Society of Australia* 2:9–16.
- KAPOS, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology* 5:173–185.
- KAUFFMAN, J. B. 1991. Survival by sprouting following fire in the tropical forests of the eastern Amazon. *Biotropica* 23:219–224.
- KAUFFMAN, J. B. & UHL, C. 1990. Interactions of anthropogenic activities, fire, and rain forests in the Amazon Basin. Pp. 117–134 in Goldammer, J. (ed). *Fire in the tropical biota*. Springer-Verlag, New York.
- KAUFFMAN, J. B., CUMMINGS, D. L., WARD, D. E. & BABBITT, R. 1995. Fire in the Brazilian Amazon: biomass, nutrient pools, and losses in slashed primary forests. *Oecologia* 104:397–408.
- KELLMAN, M. & MEAVE, J. 1997. Fire in the tropical gallery forests of Belize. *Journal of Biogeography* 24:23–34.
- KLEIN, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* 70:1715–1725.
- LAURANCE, W. F. 1998. A crisis in the making: responses of Amazonian forests to land use and climate change. *Trends in Ecology and Evolution* 13:411–415.
- LAURANCE, W. F. 2000. Do edge effects occur over large spatial scales? *Trends in Ecology and Evolution* 15:134–135.
- LAURANCE, W. F. & YENSEN, E. 1991. Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* 55:77–92.
- LAURANCE, W. F., LAURANCE, S. G., FERREIRA, L. V., RANKIN-DE MERONA, J. M., GASCON, C. & LOVEJOY, T. E. 1997. Biomass collapse in Amazonian forest fragments. *Science* 278:1117–1118.
- LAURANCE, W. F., FERREIRA, L. V., RANKIN-DE MERONA, J. M. & LAURANCE, S. G. 1998a. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79:2032–2040.
- LAURANCE, W. F., LAURANCE, S. G. & DELAMONICA, P. 1998b. Tropical forest fragmentation and greenhouse gas emissions. *Forest Ecology and Management* 110:173–180.
- LAURANCE, W. F., COCHRANE, M. A., BERGEN, S., FEARNSIDE, P. M., DELAMONICA, P., D'ANGELO, S., BARBER, C. & FERNANDES, T. 2001a. The future of the Brazilian Amazon. *Science* 291:438–439.
- LAURANCE, W. F., PEREZ-SALICRUP, D., DELAMONICA, P., FEARNSIDE, P. M., D'ANGELO, S., JEROZOLINSKI, A., POHL, L. & LOVEJOY, T. E. 2001b. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82:105–116.
- LAURANCE, W. F., LOVEJOY, T. E., VASCONCELOS, H. L., BRUNA, E., DIDHAM, R. K., STOUFFER, P. C., GASCON, C., BIERREGAARD, R. O., LAURANCE, S. G. & SAMPIAO, E. In press. Ecosystem decay of Amazonian forest fragments, a 22-year investigation. *Conservation Biology*.
- LEAN, J. & WARRILOW, D. A. 1989. Simulation of the regional climatic impact of Amazon deforestation. *Nature* 342:411–413.
- LI, H. & REYNOLDS, J. F. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. *Ecology* 75:2446–2455.
- LOVEJOY, T. E., BIERREGAARD, R. O., RYLANDS, A. B., MALCOLM, J. R., QUINTELA, C. E., HARPER, L. H., BROWN, K. S., POWELL, A. H., POWELL, G. V. N., SCHUBART, H. & HAYS, M. 1986. Edge and other effects of isolation on Amazon forest fragments. Pp. 257–285 in Soulé, M. E. (ed). *Conservation biology: the science of scarcity and diversity*. Sinauer, Sunderland.
- MAHLMAN, J. D. 1997. Uncertainties in projections of human-caused climate warming. *Science* 278:1416–1417.
- MEGGERS, B. J. 1994. Archeological evidence for the impact of mega-Niño events on Amazonian forests during the past two millennia. *Climate Change* 28:321–338.
- NEPSTAD, D. C., CARVALHO, C. R., DAVIDSON, E. A., JIPP, P. H., LEFEBVRE, P. A., NEGREIROS, P., SILVA, E. D., STONE, T. A., TRUMBORE, S. E. & VIEIRA, S. 1994. The role of deep roots in the hydrological cycles of Amazonian forests and pastures. *Nature* 372:666–669.
- NEPSTAD, D. C., MOUTINHO, P. R., UHL, C., VIEIRA, I. C. & DA SILVA, J. M. C. 1996. The ecological importance of forest remnants in an eastern Amazonian frontier landscape. Pp. 133–150

- in Schelhas, J. & Greenberg, R. (eds). *Forest patches in tropical landscapes*. Island Press, Washington, DC.
- NEPSTAD, D. C., VERISSIMO, A., ALENCAR, A., NOBRE, C., LIMA, C., LEFEBVRE, P., SCHLESINGER, P., POTTER, C., MOUTINHO, P., MENDOZA, E., COCHRANE, M. & BROOKS, V. 1999. Large-scale impoverishment of Amazonian forests by logging and fire. *Nature* 398:505–508.
- PIPERNO, D. R. & BECKER, P. 1996. Vegetational history of a site in the central Amazon Basin derived from phytolith and charcoal records from natural soils. *Quaternary Research* 45:202–209.
- ROSENFELD, D. 1999. TRMM observed first direct evidence of smoke from forest fires inhibiting rainfall. *Geophysical Research Letters* 26:3105–3108.
- SALDARRIAGA, J. & WEST, D. C. 1986. Holocene fires in the northern Amazon basin. *Quaternary Research* 26:358–366.
- SANFORD, R. L., SALDARRIAGA, J., CLARK, K., UHL, C. & HERRERA, R. 1985. Amazon rain-forest fires. *Science* 227:53–55.
- SHUKLA, J., NOBRE, C. A. & SELLERS, P. 1990. Amazon deforestation and climate change. *Science* 247:1322–1325.
- SKOLE, D. & TUCKER, C. J. 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science* 260:1905–1910.
- SUPLEE, C. 1999. El Niño/La Niña: nature's vicious cycle. *National Geographic Magazine*, March, pp. 21–34.
- TIMMERMAN, A., OBERHUBER, J., BACHER, A., ESCH, M., LATIF, M. & ROECKNER, E. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* 398:694–697.
- UHL, C. & KAUFFMAN, J. B. 1990. Deforestation effects on fire susceptibility and the potential response of the tree species to fire in the rain forest of the eastern Amazon. *Ecology* 71:437–449.
- VAN WAGNER, C. E. 1978. Age-class distribution and the forest fire cycle. *Canadian Journal of Forest Research* 8:220–227.
- WHITMORE, T. C. 1997. Tropical forest disturbance, disappearance, and species loss. Pp. 3–12 in Laurance, W. F. & Bierregaard, R. O. (eds). *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago.

