SHORT COMMUNICATION

Inferred causes of tree mortality in fragmented and intact Amazonian forests

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In fragmented tropical landscapes, among the most pervasive causes of ecological change are edge effects – diverse ecological alterations associated with the abrupt, artificial boundaries of forest fragments (Laurance & Bierregaard 1997, Lovejoy et al. 1986, Turner 1996). A striking edge effect in fragmented Amazonian forests is chronically elevated tree mortality (Ferreira & Laurance 1997, Laurance et al. 1998a). Large (> 60 cm diameter) trees are especially vulnerable to fragmentation, dying three times faster within 300 m of edges than in forest interiors (Laurance et al. 2000). Elevated tree mortality alters canopy-gap dynamics, promotes a proliferation of disturbance-adapted successional species (Laurance et al. 1998b), reduces above-ground biomass (Laurance et al. 1997), and accelerates litter production (Didham & Lawton 1999, Sizer et al. 2000) and carbon cycling (Nascimento & Laurance, in press).

At least three factors could increase tree mortality in tropical forest fragments: (1) *Microclimatic stresses*: when an edge is created, some trees simply drop their leaves and die standing (Lovejoy et al. 1986, Sizer et al. 2000), apparently because sudden changes in moisture, temperature or light (Kapos 1989, Kapos et al. 1993) exceed their physiological tolerances. (2) *Wind damage*: some trees are uprooted or snapped by winds, which accelerate over cleared land and then strike forest edges, creating increased windshear and turbulence (reviewed in Laurance, in press). Wind damage is especially

problematic for trees that grow in dense forest stands, which are poorly adapted biomechanically when exposed to forest edges (cf. Holbrook & Putz 1989, Putz et al. 1983). (3) *Proliferating lianas*: these structural parasites often increase in density near edges (Laurance et al. 2001a) and can reduce tree growth and survival (Appanah & Putz 1984, Putz 1984). Further changes, such as increased herbivory (Terborgh et al. 2001) or disease incidence in fragmented forests, are also plausible.

Aside from this list of possible causes, however, the mechanisms causing increased tree mortality in fragmented forests are poorly understood. Here we use data from a long-term study of Amazon forest dynamics to compare modes of tree death near forest edges and in forest interiors, in order to better understand the ecological pressures facing fragmented tree communities.

The study area is the 1000-km², experimentally fragmented landscape of the Biological Dynamics of Forest Fragments Project (BDFFP) in central Amazonia, 80 km N of Manaus, Brazil (2°30'S, 60°W; Lovejoy et al. 1986). Rainfall ranges from 1900–3500 mm annually with a dry season from June to October. The study area is at 50–100 m elevation and overlays heavily weathered, nutrient-poor soils (Chauvel et al. 1987). The forest canopy is closed, 30–37 m tall, with emergents to 55 m. Species richness of trees is very high and can exceed 285 species (≥ 10 cm diameter at breast height (dbh)) per hectare (Oliveira & Mori 1999).

The study area is surrounded by large expanses (> 200 km) of mainly continuous forest to the west, north and east. In the early 1980s, a series of 1-, 10- and 100-ha forest fragments were isolated by distances of 70–1000 m from surrounding forest by slashing and burning the

intervening vegetation to establish pastures in three large (*c.* 5000 ha) cattle ranches. Reserves ranging from 1–1000 ha in area were delineated in nearby continuous forest as experimental controls (cf. Lovejoy *et al.* 1986 for details).

A key component of the BDFFP is a long-term study of tree-community dynamics in fragmented and continuous forests, based on permanent 1-ha sampling plots (Laurance *et al.* 1998*a*, 2000, Rankin-de Merona *et al.* 1992). We randomly selected 16 of these plots for analysis, eight of which were near the margins of eight different fragments (three of 1 ha, three of 10 ha, two of 100 ha; with the plot centre < 100 m from forest edge in all cases) and the other eight of which were at six different sites in forest interiors (450–3000 m from the nearest edge).

Prior to fragment isolation in the early 1980s, all trees (≥ 10 cm dbh) in the plots were mapped, marked with a numbered aluminium tag, and measured for dbh (above any buttresses, if present). Following the initial census, plots were recensused repeatedly at nominal intervals of 4–6 y, with the most recent census completed in late 1999. During recensuses, the fate of each marked tree was determined. Four modes of tree death were identified: uprooted, snapped trunk, standing dead (physically intact) and other causes (e.g. possible lightning strike, unknown cause). For recently felled or standing dead trees, death was confirmed by slashing the bark to examine the vascular cambium. Clearly, some trees died after being struck by other falling trees (cf. Chambers *et al.* 2001, van der Meer & Bongers 1996) or dragged down when linked by lianas to a nearby tree that fell (e.g. Appanah & Putz 1984), but these causes could not be determined consistently. In this study, the main distinction is between trees that were killed when physically damaged versus intact, standing trees that apparently died from physiological stress or disease.

The 16 plots were studied for periods ranging from 17.2 to 19.5 y. A total of 13 229 trees were recorded in the plots, of which 2817 died during the study. The mean rate of tree mortality near forest edges ($3.67 \pm 0.70\%$ y^{-1}) was over three times higher than in forest interiors ($1.05 \pm 0.22\%$ y^{-1}), a highly significant difference ($P = 0.0002$; Mann–Whitney U-test).

Forest edges and interiors differed significantly in the relative proportions of the four modes of mortality ($\chi^2 = 24.9$, df = 3, $P < 0.0001$; chi-square test for independence). Trunk-snapping was the most common mode of mortality (Figure 1), but did not differ in frequency between edge and interior plots, causing 34–36% of all tree deaths. However, edge plots had relatively more uprooted trees, and relatively fewer standing-dead trees, than did forest interiors (both differences were significant, as the comparison was non-significant when uprooted and standing-dead trees were removed; $\chi^2 = 1.35$,
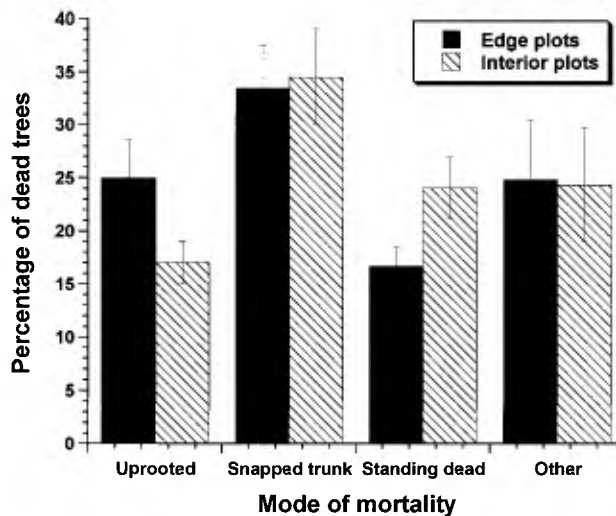

Figure 1. Mean frequency ($\pm$ 1 SE) of four modes of tree mortality in forest edges and interiors in central Amazonia (sample sizes for edge plots: uprooted, 544; snapped-trunk, 717; standing dead, 344; other causes, 521; for interior plots: uprooted: 125; snapped-trunk: 252; standing dead: 154; other causes: 160).

df = 1, P > 0.20; chi-square test for independence). The proportion of trees killed by other causes did not differ significantly between edge and interior plots (Figure 1).

We also assessed the relationship between distance to forest edge and the incidence of uprooted and standing-dead trees in each individual plot (Figure 2). Both relationships were significant, or nearly so (P < 0.06; Spearman rank correlations), confirming that edge plots often had relatively more uprooted trees, and proportionally fewer standing-dead trees.

In fragmented tropical forests, rates of tree mortality are sharply elevated near forest edges, and our results suggest that physical disturbance – either as a direct result of windshear or turbulence, or as a result of being killed or dragged down by nearby falling trees – could be the most important mechanism underlying this pattern. Wind disturbance is an important ecological force in the tropics, especially in the cyclonic and hurricane zones from about 7–20° latitude (Lugo *et al.* 1983), but also in equatorial forests affected by convectional storms (Nelson *et al.* 1994) and strong prevailing winds (Laurance, in press). Winds striking an abrupt forest edge can exert large lateral-shear forces on exposed trees and create considerable downwind turbulence for at least 2–10 times the height of the forest edge (Savill 1983, Somerville 1980). Greater windspeeds increase the persistence and frequency of wind eddies near edges that can heavily buffet the forest canopy (Bull & Reynolds 1968).

The relatively low incidence of standing dead trees near edges may indicate that microclimatic changes are of lesser importance than mechanical forces as an agent of tree death. It must be emphasized, however,
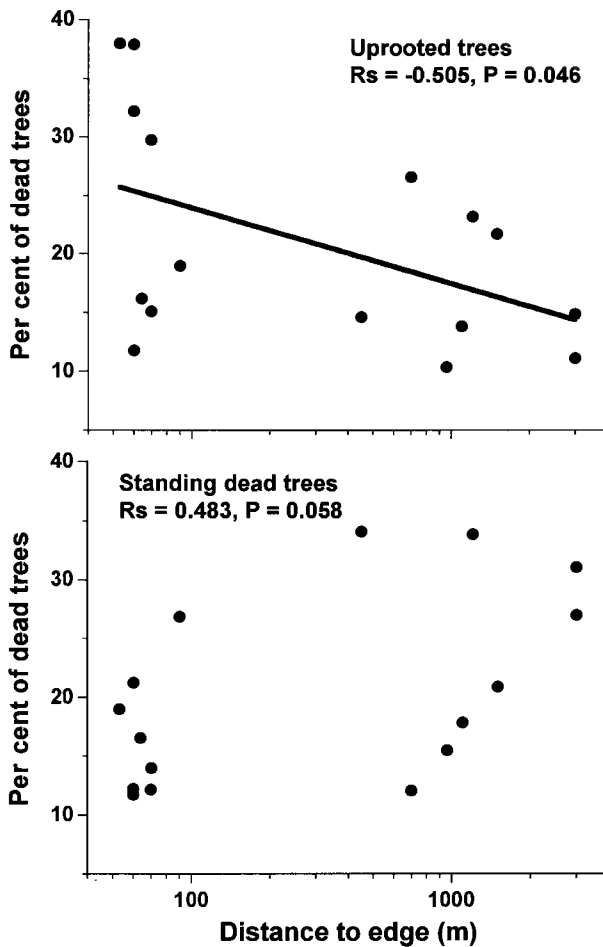
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Figure 2. Percentages of uprooted and standing-dead trees in permanent study plots in central Amazonia, as a function of distance from forest edge.

that the fragments we studied ranged from 14–18 y in age. Microclimatic stresses are clearly important during the first few years after fragmentation (Kapos 1989, Lovejoy et al. 1986, Sizer et al. 2000), when forest edges are structurally open and thereby permeable to fluxes of heat and light. After several years, however, edges tend to become sealed by a proliferation of vines and second growth, reducing the intensity of edge-related microclimatic gradients (Camargo & Kapos 1995, Kapos et al. 1993). Mortality from microclimatic stress may also decline over time because drought-sensitive trees near edges either die or become physiologically acclimated to drier edge conditions (Laurance et al. 2001b). Wind damage to forests may remain chronically elevated after fragmentation, however, as wind-tunnel models indicate that downwind turbulence should increase as edge permeability is reduced (reviewed in Laurance, in press).

Although wind damage appears to be a key cause of edge-related tree mortality in our study area, it must

be emphasized that combinations of factors, such as microclimatic stresses and increasing liana infestations, might operate in concert to predispose trees near edges to uprooting and stem breakage. It is also possible that pioneer species, which proliferate near forest edges (Laurance et al. 1998b) and often have relatively weak wood, could be especially susceptible to death from trunk snapping (Holbrook & Putz 1989, Putz et al. 1983). Because wind damage is important in fragmented forests, the provision of windbreaks (Savill 1983, Somerville 1980) or regrowth forest (Mesquita et al. 1999) near fragment margins may help to lessen edge-related tree mortality.

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