

Effects of a strong drought on Amazonian forest fragments and edges

WILLIAM F. LAURANCE*†¹, G. BRUCE WILLIAMSON†‡, PATRICIA DELAMÔNICA†, ALEXANDRE OLIVEIRA†, THOMAS E. LOVEJOY§, CLAUDE GASCON† and LUCIANO POHL†

**Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panamá*

†*Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA), C.P. 478, Manaus, AM 69011-970, Brazil*

‡*Department of Botany, Louisiana State University, Baton Rouge, LA 70803, USA*

§*Biodiversity and Conservation, Smithsonian Institution, Washington, DC 20560, USA*

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ABSTRACT. Little is known about how climatic variability affects fragmented forests and their abrupt edges. We contrasted effects of the 1997 El Niño drought between fragmented and continuous forests in central Amazonia, using long-term data on tree mortality. For 23 permanent 1-ha plots, annualized mortality rates of trees ≥ 10 cm diameter at breast height (dbh) were compared among a 'baseline' interval of 5–17 y before the drought, a 12–16-month interval during the drought, and a 12–13-month interval after the drought, using repeated-measures ANOVA. We also examined the size distributions of dead trees for each interval. During the drought, average annual tree mortality rose significantly in both forest edges (from 2.44% to 2.93%) and interiors (from 1.13% to 1.91%), and the magnitude of this increase did not differ significantly between edges and interiors. After the drought, tree mortality declined in all plots, but most dramatically on edges. Mortality rates were more variable over time on edges than interiors, and there was no evidence of time lags in mortality. In forest interiors, the size distributions of trees that died did not differ significantly among the three intervals. On edges, however, relatively fewer small (10–15 cm dbh) and more medium-sized (20–30 cm dbh) trees died in the post-drought interval, compared to other intervals. Moreover, forest edges lost a significantly higher proportion of large (≥ 60 cm dbh) trees than did forest interiors. These results suggest that droughts have relatively complex effects on fragmented Amazonian forests. Drought effects in our forest fragments probably were reduced by prior floristic and structural changes near edges and by adjoining regrowth forest that partially buffered edge vegetation from desiccating conditions.

¹ Corresponding author. Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panamá

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INTRODUCTION

The rapid pace of Amazon forest conversion is causing widespread habitat fragmentation (Laurance 1998, Skole & Tucker 1993). In fragmented habitats the amount of forest edge increases dramatically, leading to diverse physical and biotic changes (Laurance & Bierregaard 1997, Lovejoy *et al.* 1986). In rain forests dense canopy cover usually buffers the harsh external climate, but this buffering is reduced near forest edges (Kapos 1989, Williams-Linera 1990), which may result in greater mortality of drought-sensitive plants (Benitez-Malvido 1998, Sizer & Tanner 1999). In addition, wind turbulence is increased near edges, leading to additional windthrow and forest structural damage (Laurance 1997). Sharply elevated tree mortality in Amazonian forest fragments (Laurance *et al.* 1998b) causes a marked loss of living biomass that is not offset by increased growth of woody vines and small trees (Laurance *et al.* 1997, 1998a). This decline of biomass could be a significant source of atmospheric carbon emissions, released upon decay (Laurance *et al.* 1998d).

Because they are exposed to edge effects, forest fragments may be unusually vulnerable to climatic vicissitudes such as droughts. In 1997–98, the central and northern areas of the Amazon Basin experienced a strong El Niño–Southern Oscillation (ENSO) drought, among the worst this century (Hammond & ter Steege 1998, McPhaden 1999). El Niño droughts have been shown to increase tree mortality and incursions by fire into intact or logged neotropical (Condit *et al.* 1995, 1996; Cochrane *et al.* 1999, Leigh *et al.* 1990, Nepstad *et al.* 1999, Williamson *et al.* 2000) and South-East Asian (Kinnaird & O'Brien 1998, Leighton & Wirawan 1986) forests, but very little is known about their effects on isolated rain-forest fragments and forest edges. We therefore compared the effects of this unusual event on fragmented and continuous forests in the central Amazon, using long-term data on tree mortality collected before, during and after the drought.

METHODS

Study area

The study area was the experimentally fragmented landscape of the Biological Dynamics of Forest Fragments Project (BDFFP), located about 80 km north of Manaus, Brazil (2°30' S, 60° W). Rain forests in the area are evergreen and terra-firme (not seasonally flooded), ranging from *c.* 50–100 m elevation. Annual rainfall varies from about 1900–3500 mm with a pronounced dry season from June to October (Laurance 2001). The forest canopy is typically 30–37 m tall, with emergents to 55 m. The diversity of trees is very high, averaging about 280 species (≥ 10 cm dbh) per hectare (Oliveira & Mori 1999). Soils

in the study area are heavily weathered, sandy or clayey latosols, acidic and nutrient-poor, with relatively poor water-holding capacity (Laurance *et al.* 1999).

In the early 1980s, a series of forest fragments were isolated by clearing and burning the surrounding forest to create cattle pastures within three large (> 5000 ha) ranches (Bierregaard *et al.* 1992, Lovejoy *et al.* 1986). The fragments were isolated by distances of 70–650 m from continuous forest and fenced to prevent encroachment by cattle. Because of low pasture productivity, the ranches were gradually abandoned, and 3–15-m-tall secondary forests (dominated by *Cecropia* spp. and/or *Vismia* spp.) have proliferated in many cleared areas.

ENSO and rainfall

The most important factor underlying inter-annual rainfall variability in the tropics is the El Niño–Southern Oscillation (Marengo & Hastenrath 1993, Prentice & Lloyd 1998, Tian *et al.* 1998, Wright *et al.* 1999). El Niño events typically occur at 3–7-y intervals and usually are accompanied by droughts or rainfall deficits in Australasia, South Asia and much of the neotropics, with exceptionally heavy precipitation occurring along the Pacific coast of South America (Webster & Palmer 1997). Surface temperatures and insolation also increase during droughts because of reduced cloud cover (Wright *et al.* 1999). Over the past two decades, major neotropical droughts occurred in 1982–83 and 1997–98, with smaller rainfall deficits in 1987–88 and 1991–92 (Marengo *et al.* 1998, Tian *et al.* 1998).

In the Amazon Basin, El Niño droughts are most pronounced in the central and northern areas of the Basin (Hammond & ter Steege 1998, Marengo *et al.* 1998). In our central-Amazonian study area, the unusual strength of the 1997 drought is best illustrated by examining dry-season (June–October) rainfall. During the drought, dry-season rainfall was only 232 mm, less than one-third of normal (Figure 1), while the number of days without rain nearly doubled, from an average of 57 to 102 (data from BDFFP Camp Km 41). The drought ended in the central Amazon with the onset of rains in November 1997, but continued in the northern Amazon (on the opposite side of the equator, where seasons are offset by 6 mo) well into 1998 (Hammond & ter Steege 1998). Unlike the drought year, the post-drought interval in 1998–99 was quite typical: dry-season rainfall was 728 mm, which is slightly above average (698 ± 191 mm), while total annual rainfall in 1998 was slightly below average (Figure 1).

Study design

In the early 1980s, 66 permanent, square, 1-ha forest-mensuration plots were established within fragmented and continuous forests in the study area; three additional plots were added in 1991 (Laurance *et al.* 1997, 1998a; Oliveira & Mori 1999, Rankin-de Merona *et al.* 1992). Plots in fragments were protected

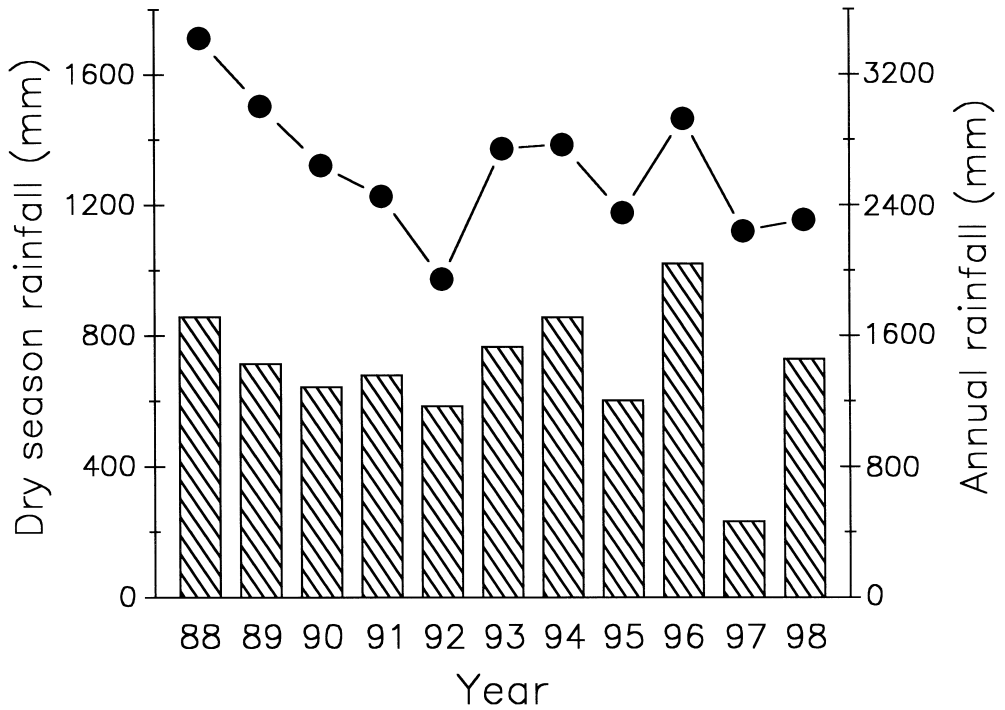


Figure 1. Dry-season rainfall (June–October, vertical bars) and total annual rainfall (filled circles) in the study area from 1988 to 1998. Data are summarized from daily rainfall records of the Biological Dynamics of Forest Fragments Project (Camp Km 41), 80 km north of Manaus, Brazil.

from fires in adjoining pastures by a 5–20 m-wide band of forest along fragment margins. Complete inventories of all trees (≥ 10 cm dbh) were conducted in each plot. Trees were marked with aluminium tags and mapped, then identified to species or morphospecies level. The plots were recensused 2–5 times to assess tree growth, recruitment, mortality and damage. Tree death was determined by an absence of foliage and lack of sap in the cambium.

By good fortune, 23 of the plots were recensused in the months immediately preceding the onset of the 1997 drought (December 1996–April 1997). These plots were evenly distributed between forest interiors and edges: there were 12 interior plots (all in continuous forest, 230–1700 m from the nearest edge, measured from the plot centre), and 11 edge plots (60–170 m from the edge, located in forest fragments of 1 ha (1 plot), 10 ha (9 plots), and on the edge of continuous forest (1 plot)). A total of 16 129 trees were enumerated in the plots.

To calculate an overall ‘baseline’ mortality rate for each plot, data from several censuses before the drought (usually conducted at 2–6-y intervals) were combined using a weighted average, so that longer censuses were given proportionately greater weight. The combined baseline interval for each plot ranged from 5.2–17.3 y (mean = 12.9 y). For each plot, the annualized rate of tree

mortality was calculated as $r = 1 - (N_t/N_o)^{1/t}$, where N_o = number of trees at beginning of interval, N_t = number of living trees at end of interval and t = number of years (Sheil *et al.* 1995).

Each plot was then recensused 12–16 mo later, in June and July of 1998, using identical methods, in order to estimate tree mortality during the 1997 drought itself. Because there could be time lags in mortality of drought-stressed trees (Pedersen 1999), we also recensused each plot in the subsequent 12–13 mo, in July and August of 1999.

There was absolutely no evidence that the length of census interval influenced mortality-rate estimates (cf. Sheil *et al.* 1995). For example, using baseline data for forest-interior plots, there was no significant correlation between mortality and census interval ($P = 0.85$, $df = 19$, $r = 0.04$). Moreover, when mortality estimates were compared for eight forest-interior plots that had both short (11–45 mo) and long (102–119 mo) census intervals, there was no significant difference ($P = 0.84$, $df = 7$, $t = 0.21$; paired t-test). Hence, no attempt was made to remove the effects of census-interval length prior to comparing mortality rates among the baseline and subsequent intervals.

Our baseline interval included earlier ENSO events, but these appear to have been less severe than the 1997 drought. Twelve of the 23 plots (including all 11 edge plots) were initially censused between 1980 and 1983, and thus may have been affected by the 1982–83 ENSO. This drought, however, appeared weaker than the 1997 ENSO, having about 16% higher dry-season (June–October) rainfall (based on records of the Brazilian National Meteorological Institute for Manaus). Likewise, the 1991–92 ENSO had far less effect on total dry-season rainfall than did the 1997 ENSO (Figure 1). Baseline mortality rates did not appear to be markedly affected by the earlier droughts; among continuous-forest plots, for example, there was very little difference in mean mortality rates ($P = 0.74$, $t = 0.35$, $df = 11$, paired t-test) between the most recent pre-drought census interval (from 1992 to early 1997; $\bar{X} \pm SD = 1.11 \pm 0.63\% y^{-1}$), which was not affected by any ENSO event, and the entire baseline interval ($1.13 \pm 0.57\% y^{-1}$), which included effects of the 1991 ENSO (a similar comparison using edge plots would have been confounded by the forest-fragmentation process in our study area). As a result, we elected to use data for the entire baseline interval in our comparisons.

Data analysis

We used a repeated-measures ANOVA to assess differences in mortality rates among the baseline, drought, and post-drought intervals, with edge distance (edge vs. interior plots) being the main effect. Our data are very appropriate for a repeated measures analysis because the same sites were sampled repeatedly using the same protocol. P values for univariate comparisons among intervals, and for the interaction between the intervals and edge distance, were adjusted using the Huynh–Feldt epsilon, in order to correct biases in the covariance matrix that can inflate F statistics (Stevens 1990). Mortality data were

log-transformed prior to analysis to reduce correlations between the mean and variance within samples. Analyses were run on Systat 7.0 (Wilkinson 1997).

RESULTS

Differences among census intervals

On average, the drought had strong effects on tree mortality (Figure 2), resulting in substantial differences among the baseline, drought and post-drought intervals ($P < 0.001$, $F_{2,42} = 15.7$; repeated-measures ANOVA). For all plots, the annualized mortality rate was significantly higher during the drought than either the baseline ($P = 0.003$, $F_{1,22} = 10.8$) or post-drought ($P < 0.001$, $F_{1,22} = 59.7$) intervals. There was no significant difference between the baseline and post-drought intervals ($P = 0.17$, $F_{1,22} = 2.0$; univariate F-tests).

Differences between edges and interiors

When combined over the three intervals, mortality was substantially higher in edge than interior plots ($P = 0.001$, $F_{1,21} = 15.7$; repeated-measures ANOVA). During the baseline interval, the annualized mortality rate near edges ($2.44 \pm 0.84\% \text{ y}^{-1}$) was more than twice that in forest interiors ($1.13 \pm 0.57\% \text{ y}^{-1}$), a

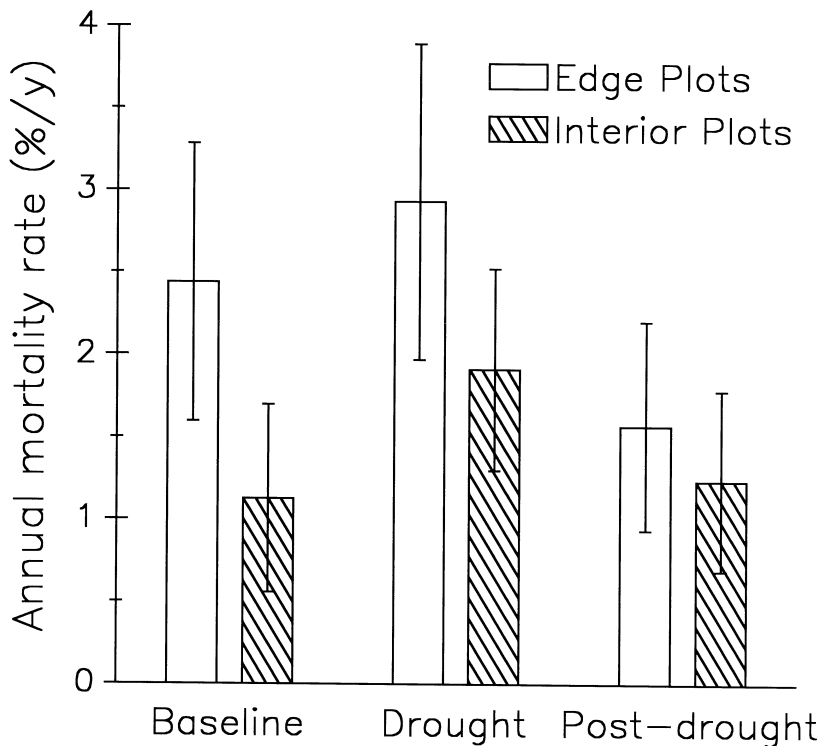


Figure 2. Mean annualized mortality rates (\pm SD) for Amazonian trees (≥ 10 cm dbh) in forest-edge and interior plots during the baseline, drought and post-drought intervals.

highly significant difference ($P < 0.001$, $F_{1,21} = 25.4$; univariate F-test). This resulted from a strong edge-to-interior gradient in tree mortality (Figure 3A).

During the drought, mortality rose both on edges (9/11 plots) and interiors (11/12 plots). The magnitude of the increase was variable among plots, averaging $0.49 \pm 1.09\%$ on edges and $0.78 \pm 0.90\%$ in interiors (Figure 2), a non-significant difference ($P = 0.51$, $F_{1,21} = 0.5$). As before, there still was an obvious edge-to-interior gradient in tree mortality (Figure 3b), with mortality again being higher in edge than interior plots ($P = 0.014$, $F_{1,21} = 7.2$; univariate F-tests). Many live trees were observed to have unusually strong leaf wilt and abscission during the drought, with leaf-fall being especially high within *c.* 60 m of forest edges.

In the year after the drought, mortality dropped in all 23 plots (Figure 2). The absolute decline was especially striking near edges, where mortality fell by $1.36 \pm 0.64\%$, compared to $0.67 \pm 0.49\%$ for interiors; this difference was significant ($P = 0.011$, $F_{1,21} = 7.7$). Because post-drought mortality declined much more sharply on edges, there was no apparent edge-to-interior gradient in tree mortality (Figure 3c) and no mean difference between edge and interior plots ($P = 0.24$, $F_{1,21} = 1.5$; univariate F-tests). This breakdown of the normal edge-to-interior mortality gradient resulted in a significant statistical interaction between time and edge distance ($P = 0.033$, $F_{2,42} = 3.9$; repeated-measures ANOVA). Nevertheless, edge plots had higher mortality rates than interior plots during all census periods (Figure 2).

Variability of forest edges

Tree mortality was considerably more dynamic over time on forest edges than interiors (Figure 2). Near edges, mortality in most (9/11) plots rose above the already-high baseline rate during the drought, then dropped sharply afterwards, with nearly all (10/11) plots falling below the baseline rate. Mortality in interior plots also increased during the drought (11/12 plots), but only half of the plots declined below the baseline rate after the drought. When the standard deviation of mortality was calculated over the three intervals for each plot (using untransformed data), edge plots had significantly higher variability (mean SD = 0.726) than did interior plots (mean SD = 0.479; $P = 0.034$, $F_{1,21} = 5.2$; univariate F-test).

Tree size distributions

Droughts may not affect trees of all sizes similarly (Condit *et al.* 1995). We therefore compared the size distributions of trees in five diameter classes (10–15, 15.1–20, 20.1–30, 30.1–59.9, ≥ 60 cm) that died during the three intervals (Figure 4). For interior plots, there was no significant difference among the intervals ($\chi^2 = 9.31$, $df = 8$, $P = 0.32$). For edge plots, however, the sizes of dead trees did vary among the intervals ($\chi^2 = 19.35$, $df = 8$, $P = 0.013$; Chi-square tests for independence), principally because relatively fewer small (10–15 cm

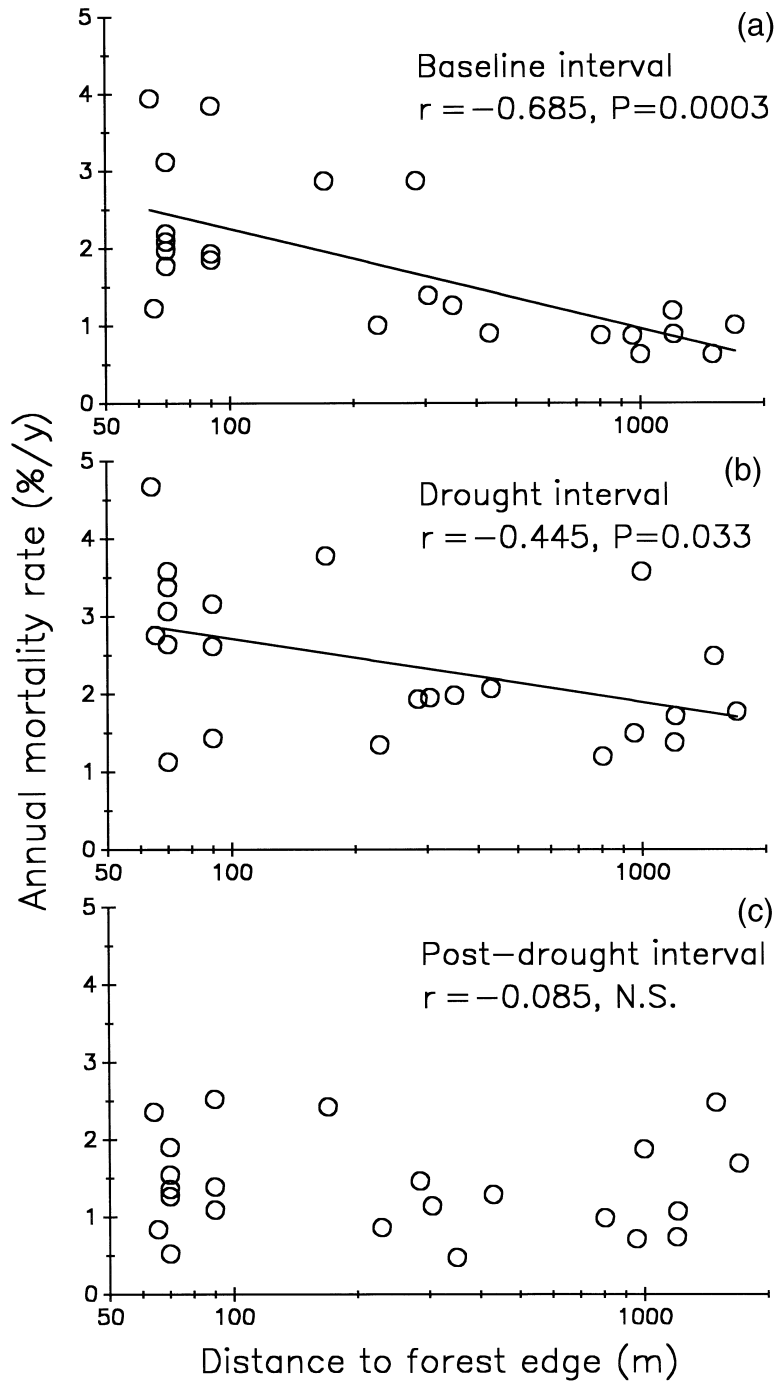


Figure 3. Relationship between annualized tree mortality and distance to forest edge during the (a) baseline, (b) drought and (c) post-drought intervals.

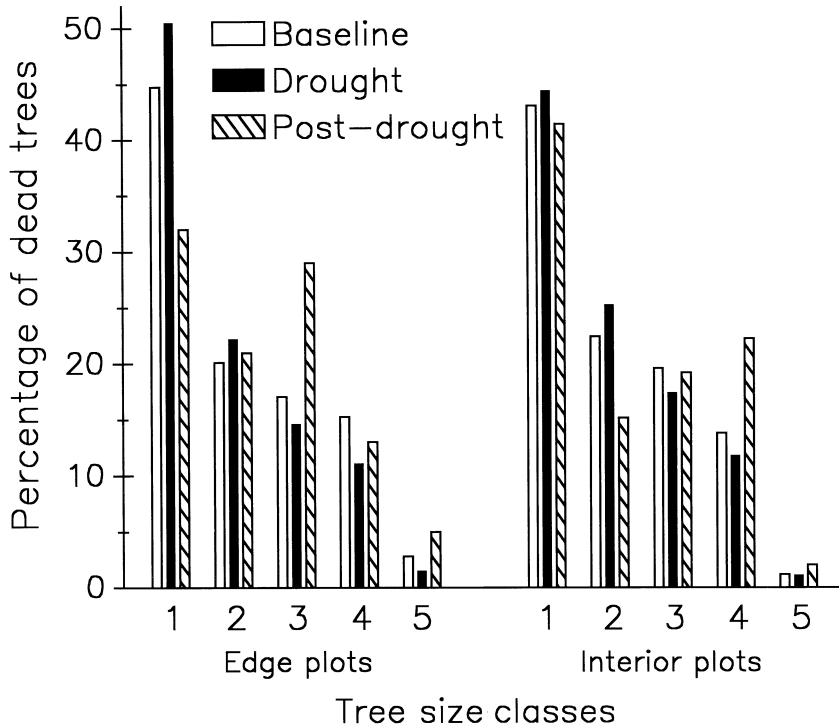


Figure 4. Size distributions of dead trees during the baseline, drought and post-drought intervals (size classes: 1 = 10–15 cm dbh; 2 = 15.1–20 cm; 3 = 20.1–30 cm; 4 = 30.1–59.9 cm; 5 = \geq 60 cm) (sample sizes: edge baseline = 1640; edge drought = 198; edge post-drought = 100; interior baseline = 776; interior drought = 178; interior post-drought = 99).

dbh) and relatively more medium-sized (20–30 cm dbh) trees died during the post-drought interval, compared to the other intervals.

There also were differences between edges and interiors. When all intervals were combined, edges lost significantly more large (\geq 60 cm dbh) trees than did forest interiors ($\chi^2 = 10.06$, $df = 4$, $P = 0.039$; Chi-square test for independence). Not only was overall mortality much higher near edges (Figure 2), but the proportion of dead trees that were large was over twice as high near edges as in forest interiors (2.79% vs. 1.23%). This difference did not arise spuriously because of intrinsic differences in large-tree density between edges and interiors: prior to fragmentation, the density of large trees did not differ significantly between edge and interior plots ($P > 0.10$, Mann-Whitney U-test).

DISCUSSION

Short-term mortality increase

Our long-term study of over 16 000 trees suggests that the 1997 ENSO drought caused a sharp but relatively short-term increase in tree mortality in both fragmented and continuous Amazonian forests. We had initially hypothesized that mortality would continue to be elevated in the year after the drought

because drought-stressed trees would continue dying at above-normal rates (cf. Pedersen 1999). In fact, we found that mortality dropped off dramatically in the post-drought interval, especially near forest edges. The most plausible explanation for this pattern is that the drought may have culled out weaker individuals, some of which would normally have died in the post-drought interval.

Drought effects in edges and interiors

It is noteworthy that tree mortality during the drought did not increase more near forest edges than interiors. We had hypothesized that forests near edges would be more vulnerable to the drought because they are exposed to hotter, drier conditions than are forest interiors (Kapos 1989, Williams-Linera 1990). Although leaf-fall was clearly elevated near edges, suggesting greater hydric stress (and also possibly reflecting prior floristic changes near edges), the mean drought-related increase in annual mortality was slightly lower near edges (from 2.44% to 2.93%) than in forest interiors (from 1.13% to 1.91%).

In our study area, several factors could have limited tree mortality near edges. First, tree communities near edges may have been somewhat 'pre-adapted' for desiccating conditions because of prior changes in floristic composition. Newly created edges experience a dramatic pulse of tree mortality (Laurance *et al.* 1997, 1998b; Lovejoy *et al.* 1986), which is soon followed by increased recruitment of pioneer and secondary species (Laurance *et al.* 1998c, Sizer & Tanner 1999). Some species proliferating on edges may be better adapted for drought conditions; for example, Condit *et al.* (1996) found that on Barro Colorado Island (BCI), Panama, moisture-demanding species declined sharply while drought-tolerant species increased, following several strong droughts in recent decades. Our forest edges were 13–17 y old at the time of the study, which is sufficient time for substantial changes in tree community composition to occur (cf. Oliveira-Filho *et al.* 1997).

In addition, older (> 5 y old) forest edges like those in our study area become partially sealed by proliferating secondary vegetation, which reduces the penetration of wind, heat and light into forests (Kapos *et al.* 1997). Finally, all of the edges in this study were surrounded by 3–15-m-tall regrowth forest, which helps to buffer edge conditions (Didham & Lawton 1999) and reduce tree mortality (Mesquita *et al.* 1999), relative to edges bordered by cattle pastures. Droughts are expected to be especially damaging to recently fragmented forests, which typically have open, unprotected edges bordered by pastures or crops, particularly in strongly seasonal areas.

Tree mortality fluctuated more dramatically near forest edges than in forest interiors. This demonstrates the dynamic nature of edge effects in this system: although tree mortality is substantially elevated near edges, it is patchy and episodic. This temporal and spatial variability apparently results from a combination of unusual weather events, like droughts and windstorms (Foster &

Terborgh 1998, Nelson *et al.* 1994), and site-specific factors such as soils, topography, edge aspect and the nature of the adjoining matrix vegetation. Because of this intrinsically high variability, short-term or small-scale studies may under- or overestimate the actual impacts of edge effects. Resource managers should consider this intrinsic variability when designing buffer zones for nature reserves (cf. Matlack 1994, Murcia 1995). Laurance & Bierregaard (1997) recommended that, to account for such inevitable uncertainties, the known penetration distance of edge effects into forests should be doubled for management purposes.

Size distributions of dead trees

The analysis of diameters of dead trees revealed two main trends. First, near forest edges, fewer small (10–15 cm dbh) and more medium-sized (20–30 cm dbh) trees died during the post-drought interval than expected. For the small trees, such a pattern might arise because some trees that would normally have died in the post-drought interval were killed by the drought; pioneer trees, for example, are often small and vulnerable to drought stress (Condit *et al.* 1995, 1996). Additional kinds of species-specific differences in drought sensitivity may well be involved, although such differences are inherently difficult to detect because most tropical tree species are rare and only trees that died were considered in our analysis. Other researchers have also had limited success in predicting the effects of ENSO droughts on plant species and functional groups in tropical forests (Becker *et al.* 1998, Condit *et al.* 1995, 1996).

The second trend is that, when edge and interior plots were compared, the former lost over twice as many large (≥ 60 cm dbh) trees as did the latter. Thus, not only did more trees die on edges, but a higher proportion of the dying trees were large (this effect was evident for all three census intervals, especially the baseline and post-drought intervals; Figure 4). There are at least four possible reasons for this pattern. First, because of their tall stature, canopy and emergent trees may be particularly vulnerable to windshear and turbulence effects near forest edges (Laurance 1997). Second, large, old trees are especially prone to infestation by lianas, which rise markedly in abundance near forest edges (Laurance *et al.* 2001a) and can increase tree mortality and windthrow (Putz 1984). Third, large trees may be prone to desiccation stress near edges, possibly because their crowns are exposed to intense sunlight and evaporation; canopy and emergent trees experienced higher mortality than smaller trees during droughts in Asian (Leighton & Wirawan 1986), African (Swaine 1992) and neotropical (Condit *et al.* 1995) forests. Finally, lightning strikes may be a significant cause of Amazonian tree mortality (Magnusson *et al.* 1996), and large trees in isolated fragments might attract lightning more frequently than do those in large forest tracts.

The decline of large trees in fragmented forests has many implications (Laurance *et al.* 2000a). Because large trees contain a high proportion of forest biomass (Clark & Clark 1995), their rapid loss partly underlies the sharp

decline of living biomass in fragments (Laurance *et al.* 1997, 1998a), which may be a significant source of greenhouse gas emissions (Laurance *et al.* 1998d). Large tropical trees can vary in age from a century to well over a thousand years old (Chambers *et al.* 1998, Condit *et al.* 1995, Martínez-Ramos & Alvarez-Buylla 1998, Williamson *et al.* 1999), and thus can require very extensive periods for replacement, especially if elevated tree mortality is chronic in fragments (Laurance *et al.* 1998a). Forest volume may be reduced in fragmented forests, with tall, structurally complex forests being replaced by shorter, scrubrier forests. The size and age distributions of forests will tend to shift toward smaller and younger individuals. Forest turnover rates may well accelerate if long-lived trees are replaced by shorter-lived pioneer and secondary species (Laurance *et al.* 1998b, c; Tabarelli *et al.* 1999).

Conclusions and implications

The strong 1997 ENSO drought caused a moderate, short-term increase in tree mortality in our study area. The hypothesis that forests near edges would suffer greater drought-related mortality than forest interiors was not supported, and this may have resulted from prior floristic and structural changes in edge and adjoining matrix vegetation that helped to buffer fragments from desiccating conditions.

Tree mortality was more dynamic near forest edges than interiors, and the size distributions of dying trees varied significantly over time on edge plots. Such changes could potentially promote differences in floristic composition between edge and interior vegetation, leading to a progressive increase of desiccation-tolerant species in fragments.

Our results probably do not apply to extensive seasonal forests of the Amazon, such as those in the eastern, southern, and north-central areas of the basin, which appear much more strongly affected by droughts than do those in our study area. These drier areas are experiencing very high rates of forest fragmentation and logging (Laurance *et al.* 2001b, Nepstad *et al.* 1999, Skole & Tucker 1993), which sharply increase the vulnerability of forests to destructive wildfires during droughts (Cochrane *et al.* 1999, Nepstad *et al.* 1998). Droughts and fires may increase in the Amazon because rainfall is likely to be reduced by further deforestation (which reduces regional evapotranspiration; Lean & Warrilow 1989, Shukla *et al.* 1990) and by smoke from forest fires (which traps atmospheric moisture; Rosenfeld 1999). Moreover, some leading global-circulation models suggest that extreme weather events, such as ENSO droughts and tropical storms, will increase in frequency or severity as a result of global warming (IPCC 1996, Mahlman 1997, Timmerman *et al.* 1999). As a result, the impacts of droughts on Amazonian forests could become more severe in the future.

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LITERATURE CITED

- BECKER, P., ONG, C. L. & GOH, F. 1998. Selective drought mortality of dipterocarp trees: no correlation with timber group distributions in Borneo. *Biotropica* 30:666–671.
- BENTITEZ-MALVIDO, J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conservation Biology* 12:380–389.
- BIERREGAARD, R. O., LOVEJOY, T. E., KAPOV, V., DOS SANTOS, A. A. & HUTCHINGS, R. W. 1992. The biological dynamics of tropical rain forest fragments. *BioScience* 42:859–866.
- CHAMBERS, J. Q., HIGUCHI, N. & SCHIMMEL, J. 1998. Ancient trees in Amazonia. *Nature* 391:135–136.
- CLARK, D. B. & CLARK, D. A. 1995. Abundance, growth and mortality of very large trees in neotropical lowland rain forest. *Forest Ecology and Management* 80:235–244.
- COCHRANE, M. A., ALENCAR, A., SCHULZE, M. D., SOUZA, C. M., NEPSTAD, D. C., LEFEBVRE, P. & DAVIDSON, E. A. 1999. Positive feedbacks in the fire dynamics of closed canopy tropical forests. *Science* 284:1832–1835.
- CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* 65:419–439.
- CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 1996. Assessing the responses of plant functional types to climate change in tropical forests. *Journal of Vegetation Science* 7:405–416.
- DIDHAM, R. K. & LAWTON, J. H. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31:17–30.
- FOSTER, M. S. & TERBORGH, J. 1998. Impact of a rare storm event on an Amazonian forest. *Biotropica* 30:470–474.
- HAMMOND, D. S. & TER STEEGE, H. 1998. Propensity for fire in Guianan rain forests. *Conservation Biology* 12:944–947.
- IPCC 1996. *Climate change 1995: impacts, adaptations and mitigation of climate change. Summary for policy makers*. Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge. 56 pp.
- KAPOV, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology* 5:173–185.
- OS, V., WANDELLI, E., CAMARGO, J. L. & GANADE, G. 1997. Edge-related changes in environment and plant responses due to forest fragmentation in central Amazonia. Pp. 33–44 in Laurance, W. F. & Bierregaard, R. O. (eds). *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago.
- KINNAIRD, M. F. & O'BRIEN, T. G. 1998. Ecological effects of wildfire on lowland rain forest in Sumatra. *Conservation Biology* 12:954–956.
- LAURANCE, W. F. 1997. Hyper-disturbed parks: edge effects and the ecology of isolated rain forest reserves in tropical Australia. Pp. 71–83 in Laurance, W. F. & Bierregaard, R. O. (eds). *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago.
- 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. 2001. The hyper-diverse flora of the central Amazon: an overview. Pp. 47–53 in Bierregaard, R. O., Gascon, C., Lovejoy, T. E. & Mesquita, R. (eds). *Lessons from Amazonia: ecology and conservation of a fragmented forest*, Yale University Press, New Haven.
- LAURANCE, W. F. & BIERREGAARD, R. O., eds. 1997. *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago. 616 pp.
- LAURANCE, W. F., COCHRANE, M. A., BERGEN, S., FEARNSIDE, P. M., DELAMONICA, P., BARBER, C., D'ANGELO, S. & FERNANDES, T. 2001b. The future of the Brazilian Amazon. *Science* 291:438–439.
- LAURANCE, W. F., DELAMONICA, P., LAURANCE, S. G., VASCONCELOS, H. L. & LOVEJOY, T. E. 2000a. Rainforest fragmentation kills big trees. *Nature* 404:836.
- LAURANCE, W. F., FEARNSIDE, P. M., LAURANCE, S. G., DELAMONICA, P., LOVEJOY, T. E., RANKIN-DE MERONA, J. M., CHAMBERS, J. Q. & GASCON, C. 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. *Forest Ecology and Management* 118:127–138.

- LAURANCE, W. F., FERREIRA, L. V., GASCON, C. & LOVEJOY, T. E. 1998a. Biomass decline in Amazonian forest fragments. *Science* 282:1611a.
- LAURANCE, W. F., FERREIRA, L. V., RANKIN-DE MERONA, J. M. & LAURANCE, S. G. 1998b. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79:2032–2040.
- LAURANCE, W. F., FERREIRA, L. V., RANKIN-DE MERONA, J. M., LAURANCE, S. G., HUTCHINGS, R. & LOVEJOY, T. E. 1998c. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology* 12:460–464.
- LAURANCE, W. F., LAURANCE, S. G. & DELAMÓNICA, P. 1998d. Tropical forest fragmentation and greenhouse gas emissions. *Forest Ecology and Management* 110:173–180.
- 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., PEREZ-SALICRUP, D., DELAMÓNICA, P., FEARNSIDE, P. M., JEROZOLINSKI, A., D'ANGELO, S. & LOVEJOY, T. E. 2001a. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82:105–116.
- LEAN, J. & WARRILOW, D. A. 1989. Simulation of the regional climatic impact of Amazon deforestation. *Nature* 342:411–413.
- LEIGH, E. G., WINDSOR, D. M., RAND, A. S. & FOSTER, R. B. 1990. The impact of the 'El Niño' drought of 1982–83 on a Panamanian semideciduous forest. Pp. 473–486 in Glynn, P. W. (ed.). *Global ecological consequences of the 1982–83 El Niño–Southern Oscillation*. Elsevier, Amsterdam.
- LEIGHTON, M. & WIRAWAN, N. 1986. Catastrophic drought and fire in Borneo tropical rain forest associated with the 1982–1983 El Niño–Southern Oscillation event. Pp. 75–102 in Prance, G. T. (ed.). *Tropical rain forests and the world atmosphere*. AAAS Symposium 10, Boulder.
- 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. O. R. & HAYS, M. B. 1986. Edge and other effects of isolation on Amazon forest fragments. Pp. 257–285 in Soule, M. E. (ed.). *Conservation biology: the science of scarcity and diversity*. Sinauer, Sunderland.
- MAGNUSSON, W. E., LIMA, A. P. & LIMA, O. P. 1996. Group lightning mortality of trees in a neotropical forest. *Journal of Tropical Ecology* 12:899–903.
- MAHLMAN, J. D. 1997. Uncertainties in projections of human-caused climate warming. *Science* 278:1416–1417.
- MARENGO, J. A. & HASTENRATH, S. 1993. Case studies of extreme climatic events in the Amazon Basin. *Journal of Climate* 6:617–627.
- MARENGO, J. A., TOMASELLA, J. & UVO, C. R. 1998. Trends in streamflow and rainfall in tropical South America: Amazonia, eastern Brazil, and northwestern Peru. *Journal of Geophysical Research* 103:1775–1783.
- MARTÍNEZ-RAMOS, M. & ALVAREZ-BUYLLA, E. R. 1998. How old are tropical rain forest trees? *Trends in Plant Science* 3:400–405.
- MATLACK, G. R. 1994. Plant demography, land-use history, and the commercial use of forests. *Conservation Biology* 8:298–299.
- McPHADEN, M. J. 1999. The child prodigy of 1997–98. *Nature* 398:559–562.
- MESQUITA, R., DELAMÓNICA, P. & LAURANCE, W. F. 1999. Effects of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biological Conservation* 91:129–134.
- MURCIA, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10:58–62.
- NELSON, B. W., KAPOS, V., ADAMS, J. B., OLIVEIRA, W. J., BRAUN, O. P. & DO AMARAL, I. L. 1994. Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology* 75:853–858.
- NEPSTAD, D. C., MOREIRA, A., VERISSIMO, A., LEFEBVRE, P., SCHLESINGER, P., POTTER, C., NOBRE, C., SETZER, A., KRUG, T., BARROS, A., ALENCAR, A. & PEREIRA, J. 1998. Forest fire prediction and prevention in the Brazilian Amazon. *Conservation Biology* 12:951–955.
- NEPSTAD, D. C., VERISSIMO, A., ALENCAR, A., NOBRE, C., LIMA, E., 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.
- OLIVEIRA, DE, A. A. & MORI, S. A. 1999. A central Amazonian terra firme forest. I. High tree species richness on poor soils. *Biodiversity and Conservation* 8:1219–1244.
- OLIVEIRA-FILHO, A. T., DE MELLO, J. M. & SCOLFORO, J. R. S. 1997. Effects of past disturbance and edges on tree community structure and dynamics within a fragment of tropical semideciduous forest in south-eastern Brazil over a five-year period (1987–1992). *Plant Ecology* 131:45–66.
- PEDERSEN, B. S. 1999. The mortality of midwestern overstory oaks as a bioindicator of environmental stress. *Ecological Applications* 9:1017–1027.
- PRENTICE, I. C. & LLOYD, J. 1998. C-quest in the Amazon Basin. *Nature* 396:619–620.
- PUTZ, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65:1713–1724.
- RANKIN-DE MERONA, J. M., PRANCE, G. H., HUTCHINGS, R., SILVA, M., RODRIGUES, W. &

- UEHLING, M. 1992. Preliminary results of a large-scale inventory of upland rain forest in the central Amazon. *Acta Amazonica* 22:493–534.
- ROSENFELD, D. 1999. TRMM observed first direct evidence of smoke from forest fires inhibiting rainfall. *Geophysical Research Letters* 26:3105–3108.
- SHUKLA, J., NÓBRE, C. A. & SELLERS, P. 1990. Amazon deforestation and climate change. *Science* 247:1322–1325.
- SIZER, N. & TANNER, E. V. J. 1999. Responses of woody plant seedlings to edge formation in a lowland rain forest, Amazonia. *Biological Conservation* 91:135–142.
- SHEIL, D., BURSLEM, D. & ALDER, D. 1995. The interpretation and misinterpretation of mortality rate measures. *Journal of Ecology* 83:331–333.
- SKOLE, D. & TUCKER, C. J. 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science* 260:1905–1910.
- STEVENS, J. 1990. *Intermediate statistics: a modern approach*. Lawrence Erlbaum, Hillsdale.
- SWAINE, M. D. 1992. Characteristics of dry forest in West Africa and the influence of fire. *Journal of Vegetation Science* 3:365–374.
- TABARELLI, M., MANTOVANI, W. & PERES, C. A. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation* 91:119–127.
- TIAN, H., MELILLO, J. M., KICKLIGHTER, D. W., MCGUIRE, A., HELFRICH, J., MOORE, W. & VOROSMARTY, C. 1998. Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature* 396:664–667.
- 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.
- WEBSTER, P. J. & PALMER, T. N. 1997. The past and the future of El Niño. *Nature* 390:562–564.
- WILKINSON, L. 1997. *Systat 7.0*. Systat, Inc., Evanston. 449 pp.
- WILLIAMS-LINERA, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology* 78:356–373.
- WILLIAMSON, G. B., LAURANCE, W. F., OLIVEIRA, A. A., DELAMÔNICA, P., LOVEJOY, T. E., GASCON, C. & POHL, L. 2000. Amazonian wet forest resistance to the 1997–98 El Niño drought. *Conservation Biology* 14:1538–1542.
- WILLIAMSON, G. B., VAN ELDIK, T., DELAMÔNICA, P. & LAURANCE, W. F. 1999. How many millenarians in Amazonia: sizing the ages of large trees. *Trends in Plant Science* 10:387.
- WRIGHT, S. J., CARRASCO, C., CALDERÓN, O. & PATON, S. 1999. The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80:1632–1642.

