

SHORT COMMUNICATION

Rain-forest fragmentation and the phenology of Amazonian tree communities

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Habitat fragmentation affects the ecology of tropical rain forests in many ways, such as reducing species diversity of many taxa (Laurance *et al.* 2002, Lovejoy *et al.* 1986) and increasing rates of tree mortality and canopy-gap formation near forest edges (Laurance *et al.* 1997, 1998, 2001). Such obvious alterations have been documented in many fragmented forests, but more subtle changes, such as those affecting plant phenology (the timing and frequency of flower, fruit and leaf production), have received far less attention. Adler & Kiepiniski (2000) showed that different populations of the successional tree *Spondias mombin* on small man-made islands in Panama had highly synchronous flowering and fruiting. In montane forests in Colombia, Restrepo *et al.* (1999) demonstrated that understory fruit abundance was consistently increased over time near forest edges relative to forest interiors. Beyond these and a few other studies (Ackerly *et al.* 1990, Nason & Hamrick 1997), however, the effects of fragmentation on plant phenology have been inadequately assessed, especially in the tropics.

In a recently fragmented Amazonian forest, we assessed the influence of edge effects and tree size on the incidence of flowering, fruiting, leaf production and leaf shedding in 14 species of canopy and emergent trees over a 2-y period. We postulated that increased sunlight and hence photosynthetic energy near forest–pasture edges would promote more frequent flowering, fruiting (Aldrich & Hamrick 1998, Wright & van Schaik 1994),

and leaf production (Lovejoy *et al.* 1986), whereas higher desiccation and light intensities near edges would lead to increased leaf shedding (Sizer & Tanner 1999).

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 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.

In the early 1980s, a long-term study of tree-community dynamics was initiated in fragmented and continuous forests in the study area based on 69 square 1-ha plots and 13 ha of 40-m-wide belt transects (Rankin-de Merona *et al.* 1992). Within each plot and transect, all trees (≥ 10 cm dbh) were mapped to the nearest 0.1 m, marked with a numbered aluminium tag, and measured for dbh (above

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any buttresses, if present). Sterile or fertile material for each tree is lodged at the BDFFP Herbarium.

This study was conducted in 1985 and 1986 in four 1-ha fragments, three 10-ha fragments and one 100-ha fragment, and in seven control sites in the interior of nearby continuous forest (700–3000 m from the nearest forest edge). A total of 34.38 ha of plots or transects was sampled in the eight fragments (1 ha each in the four 1-ha fragments; 5.0, 5.06 and 10.24 ha, respectively, in the three 10-ha fragments; 10.08 ha in the 100-ha fragment), and 15.68 ha in continuous forest. At the beginning of this study, all fragments were < 5 y old (three were 6 mo old, three were 1.5 y old, and two were 4.5 y old).

We focused on 14 species (840 individuals) of canopy or emergent trees that could be readily identified in the field and were not overly rare (with mean densities of 0.3–4.0 stems ha⁻¹). Phenological observations were recorded for each tree at bimonthly intervals (January, March, May, July, September, November), beginning in January 1985 and ending in November 1986. During each of 12 observations, visual surveys using binoculars were used to determine the presence or absence of (1) flowers (buds or open flowers present on the tree, or buds or floral parts on the ground at the tree base); (2) fruits (immature or mature fruits in the crown, or mature or old fruits or seeds at the tree base); (3) new leaf production; and (4) leaf shedding (indicated by leafless branches or crowns). Data on tree mortality and dbh were also recorded in each survey, and trees that died were excluded from that and any subsequent surveys.

The 14 tree species represent five families. Most are canopy or emergent trees that rely on insect or bat pollinators and vertebrate seed dispersers; none is known to be dioecious or deciduous. These species often require canopy openings for successful recruitment and many have been recorded in secondary forests, although all are typical of primary rain forest (Ribeiro *et al.* 1999; N. Lepsch-Cunha, *pers. comm.*). The studied species are *Caryocar glabrum*, *C. pallidum* (both Caryocaraceae); *Goupia glabra* (Celastraceae); *Casearia javitensis* (Flacourtiaceae); *Corythophora alta*, *C. rimosa*, *Eschweilera atropetiolata*, *Lecythis barnebyi*, *L. poiteaui*, *L. prancei* (all Lecythidaceae); *Dipteryx odorata*, *Swartzia polyphylla*, *S. reticulata* and *Eperua glabriflora* (all Leguminosae).

Data from the bimonthly censuses were used to determine whether each species exhibited flowering, fruiting, leaf production or leaf shedding during the study, yielding a 0–2 response variable (0 = no observations; 1 = observations during one year; 2 = observations during both years). Multiple logistic regression analysis was used to test the effects on each response variable of two independent factors: (1) tree diameter (dbh), which is positively correlated with flowering and fruiting in at least some tropical trees (e.g. Adler & Kiepinski 2000, Thomas 1996); and (2) the

linear distance of the tree to the nearest forest–pasture edge (log₁₀-transformed), which was assessed because tree communities in recently fragmented Amazonian forests are clearly affected by greater desiccation, windshear and liana infestations within 60–300 m of forest edges (Laurance *et al.* 1997, 1998, 2000, 2001; Lovejoy *et al.* 1986).

Rainfall patterns were not atypical during the study. In both years, dry-season (June–October) rainfall was slightly (553–574 mm) above the long-term average ($\bar{X} \pm \text{SD} = 458 \pm 124$ mm from 1968–1998), whereas wet-season (November–May) rainfall (1890–1918 mm) was near normal (1854 ± 269 mm).

Tree diameter often had a significant ($P \leq 0.05$) and positive effect on flowering and fruiting frequency. Eight species exhibited positive effects of tree size on flowering, whereas six species showed similar effects on fruiting (Table 1). Tree diameter had a significant, negative effect on leaf production in two species, and no significant effects on leaf shedding (Table 1).

Distance to forest edge had significant ($P \leq 0.05$) effects on only four species (Table 1). Flowering frequency was significantly reduced near edges in two species (*E. glabriflora* (Figure 1), *L. prancei*), whereas fruiting was significantly reduced near edges in *C. glabrum* and significantly increased near edges in *Swartzia reticulata*. Leaf production was significantly increased near edges in *S. reticulata*, but distance to edge had no significant effects on leaf shedding.

If a Bonferroni-corrected alpha value is used ($P = 0.011$), then tree size had significant, positive effects on flowering and fruiting frequency in seven and five species, respectively, but did not significantly affect leaf production or shedding (Table 1). Distance to forest edge had only one significant effect, with flowering frequency declining near edges in *E. glabriflora*.

Our findings provide little support for the notion that tree reproduction will generally increase near forest edges. Rather, only a few species responded significantly to edges and most of these had less frequent flowering or fruiting. One potential cause of reduced plant reproduction in fragmented forests is a decline of key pollinators that leads to reduced seed set (Aizen & Feinsinger 1994, Nason & Hamrick 1997). This possibility cannot be entirely discounted in this study because many Amazonian invertebrate species respond negatively to fragmentation and edge effects (Brown & Hutchings 1997, Didham *et al.* 1998, Powell & Powell 1987). However, a more likely explanation is that many trees appear to be physiologically stressed by higher temperatures and evapotranspiration near forest edges (Didham & Lawton 1999, Kapos *et al.* 1997), and that these stresses reduce reproduction in some species. Microclimatic alterations are most severe in recently fragmented forests (Kapos *et al.* 1997), as in this study, where forest edges are structurally

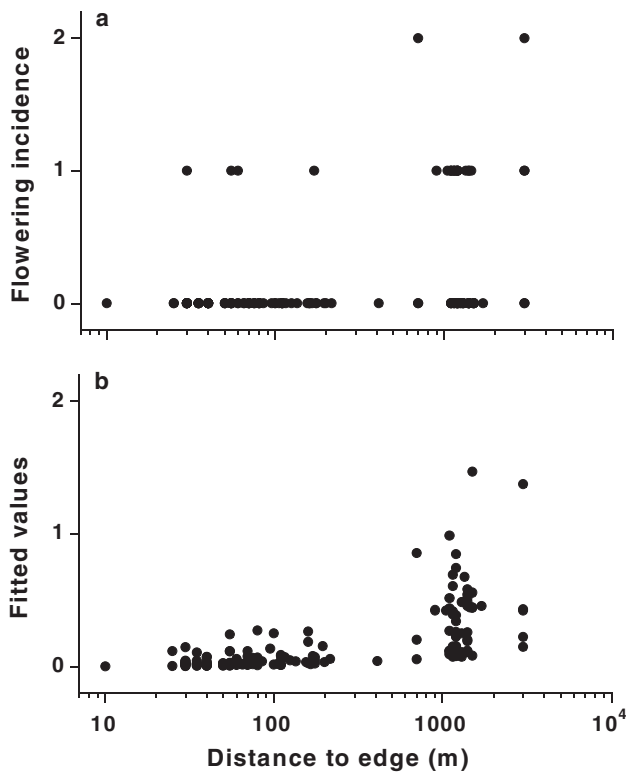


Figure 1. Relationship between (a) flowering incidence over a 2-y period and distance to forest edge for 150 individuals of the Amazonian tree *Eperua glabriflora*. (b) Fitted values for a multiple logistic regression model with the same data, using distance to forest edge and tree diameter as predictors.

open and plants have had little time to become physiologically acclimated to edge conditions. Such stresses overwhelm many rain-forest trees, which simply drop their leaves and die standing during the first few months or years after edge creation (Lovejoy *et al.* 1986). During this 2-y study, mortality rates of the 840 trees we mon-

itored were over twice as high within 100 m of forest edges (3.73% y^{-1}) as further from edges (1.64% y^{-1}), a highly significant difference ($G = 7.19$, $df = 1$, $P = 0.008$; G -test).

We also found little evidence that leaf production and shedding were altered near edges. We had particularly expected leaf shedding to increase near edges, both because of greater desiccation and because shade-adapted understorey leaves (Bazzaz 1991) might be shed in response to greater light intensity near edges. Notably, leaf shedding clearly rose near forest edges in our study area during the major 1997 El Niño drought, when dry-season rainfall was less than a third of normal (Laurance & Williamson 2001).

Not surprisingly, tree size had a positive effect on flowering or fruiting frequency in over half of the species we examined, a trend also observed in other studies (Adler & Kiepiniski 2000, Bullock & Bawa 1981, Lepsch-Cunha & Mori 1999). Quite apparently, photosynthetic resources needed for reproduction are often not available to trees until they reach the canopy, where access to light increases dramatically (Thomas 1996).

Although edge effects had only a limited influence on tree reproduction in this study, it must be emphasized that many tropical tree species reproduce supra-annually and that some produce flowers and fruit for periods of just a few weeks (Ackerly *et al.* 1990, Adler & Kiepiniski 2000, Bullock & Bawa 1981). As a consequence, we may have underestimated the incidence of reproduction in this study because tree phenology was assessed at bimonthly intervals and for just 2 y.

Even if tree phenology is not being markedly altered, forest fragmentation could still have serious effects on tree reproduction. This is because large (≥ 60 cm dbh) canopy and emergent trees are especially vulnerable to fragmentation, dying nearly three times faster within 300

Table 1. Summary of multiple logistic regression models used to assess the influence of tree diameter (dbh) and distance to forest edge (ed) on the incidence of flowering, fruiting, leaf production and leaf shedding in central Amazonian trees over a 2-y period (+ and - indicate significant positive and negative effects, respectively; alpha values are in parentheses; N = number of trees). Dashed lines indicate that the incidence of production or shedding was too low to permit regression analysis.

Species	Flowering		Fruiting		Leaf production		Leaf shedding		N
	dbh	ed	dbh	ed	dbh	ed	dbh	ed	
<i>Caryocar glabrum</i> (Aubl.) Pers.	+(0.054)		+(0.002)	+(0.05)					21
<i>C. pallidum</i> A. C. Sm.	+(0.0003)		+(0.0015)						34
<i>Casearia javitensis</i> Kunth							---	---	22
<i>Corythophora alta</i> R. Knuth	+(<0.0001)		+(0.0001)			-(0.043)			130
<i>C. rimosa</i> W. A. Rodrigues	+(0.0003)		+(0.046)				---	---	52
<i>Dipteryx odorata</i> (Aubl.) Willd.	---	---					---	---	19
<i>Eperua glabriflora</i> (Ducke) R. S. Cowan	+(0.0001)	+(0.0001)	+(0.0007)			-(0.023)			150
<i>Eschweilera atropetiolata</i> S. A. Mori							---	---	21
<i>Goupia glabra</i> Aubl.			+(0.008)						82
<i>Lecythis barnebyi</i> S. A. Mori	+(0.01)								48
<i>L. poiteaui</i> O. Berg	+(0.038)								23
<i>L. prancei</i> S. A. Mori	+(0.003)	+(0.049)							25
<i>Swartzia polyphylla</i> DC.	---	---	---	---					15
<i>S. reticulata</i> Ducke				-(0.017)		-(0.043)			198

m of edges than in forest interiors (Laurance *et al.* 2000). Large trees are often reproductively dominant and are important sources of food and shelter for animal populations (Richards 1998), and thus their decline could have important impacts on fragment ecology. Hence, even if edge effects have a limited influence on tree reproduction in the initial years after fragment isolation, fragmentation could have serious longer-term effects because of the striking decline over time of large, reproductively dominant trees.

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