

# Apparent environmental synergism drives the dynamics of Amazonian forest fragments

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**Abstract.** Many contemporary ecosystems are likely to be affected by multiple environmental drivers, complicating efforts to predict future changes in those ecosystems. We studied long-term changes (1980–2012) in forest dynamics and liana (woody vine) abundance and biomass in fragmented and intact forests of the central Amazon. We did so by contrasting trends in 33 permanent 1-ha plots near forest edges (plot center <100 m from the nearest edge) with those in 36 1-ha plots in intact-forest interiors (150–3300 m from nearest edge). In fragmented and edge-affected forests, rates of tree ( $\geq 10$  cm diameter at breast height) mortality and recruitment were often sharply elevated, especially in the first 10–15 years after fragmentation. Lianas ( $\geq 2$  cm stem diameter) also increased markedly in abundance (mean  $\pm$  SD =  $1.78 \pm 1.23\%$  per yr) and biomass ( $1.30 \pm 1.39\%$  per yr) over time, especially in plots with high edge-related tree mortality. However, plots in undisturbed forest interiors, which were originally established as experimental controls, also experienced long-term changes. In these plots, tree mortality and recruitment rose significantly over time, as did liana abundance ( $1.00 \pm 0.88\%$  per yr) and biomass ( $0.32 \pm 1.37\%$  per yr). These changes were smaller in magnitude than those in fragments but were nonetheless concerted in nature and highly statistically significant. The causes of these changes in forest interiors are unknown, but are broadly consistent with those expected from rising atmospheric CO<sub>2</sub> or regional climate drivers that influence forest dynamics. Hence, the dynamics of Amazonian forest fragments cannot be understood simply as a consequence of forest fragmentation. Rather, the changes we observed appear to arise from an interaction of fragmentation with one or more global- or regional-scale drivers affecting forest dynamics. Both sets of phenomena are evidently increasing forest dynamics and liana abundances in fragmented forests, changes that could reduce carbon storage and alter many aspects of forest ecology.

**Key words:** Amazon; biomass; carbon storage; CO<sub>2</sub> fertilization; environmental synergism; forest dynamics; global change; habitat fragmentation; lianas; tree mortality; tree recruitment; woody vines.

## INTRODUCTION

The Earth is being affected by myriad anthropogenic influences (Lewis et al. 2004a, 2009a), such that any particular locale could easily be influenced by two or more environmental changes occurring concurrently. In the tropics, for instance, vast expanses of forest are being cleared and fragmented, and many remaining forests are also being selectively logged, damaged by surface fires, or perturbed by hunting (Cochrane and Laurance 2002, Michalski and Peres 2007). Disruption of forest cover can also alter land–atmosphere interactions and local precipitation (Laurance 2004), whereas forest desiccation can be promoted by large-scale edge

effects (Briant et al. 2010) and moisture-trapping smoke from biomass burning (Rosenfeld 1999). At larger spatial scales, increases in global temperature could potentially influence tropical rainfall regimes (Lewis et al. 2011, Fu et al. 2013) and storm intensity (Knutson et al. 2010), whereas rising atmospheric CO<sub>2</sub> concentrations, increased nutrient deposition from air pollution, and other factors might affect forest productivity and dynamics (Phillips and Gentry 1994, Lewis et al. 2009a).

The realization that ecosystems are often being affected by multiple environmental changes raises an obvious possibility that certain stressors might amplify or reinforce one another. The term “environmental synergism” is often used to connote such effects. Strictly speaking, this term implies that the net impact of two or more stressors is greater than the sum of each acting individually (Zala and Penn 2004), but it is often used simply to indicate that simultaneous stressors are

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operating roughly in concert or that one stressor facilitates another (e.g., Myers 1986, Laurance and Useche 2009). Two notable synergisms in the tropics are those between habitat fragmentation and fire (Cochrane and Laurance 2002), and between selective logging and hunting (Poulsen et al. 2011). Here we extend current knowledge by describing an apparent synergism between habitat fragmentation and global or regional-scale drivers affecting Amazonian forests.

We focus on the stand-level dynamics of trees and lianas (woody vines), which collectively account for much of the physical structure, floristic diversity, and primary productivity of tropical forests. Lianas are important competitors and structural parasites of tropical trees, exploiting them for physical support to reach the forest canopy. By physically stressing trees and competing for light, nutrients, and water, liana infestations can reduce tree growth, fecundity, survival, and recruitment (Putz 1984, Stevens 1987, Schnitzer et al. 2000, Schnitzer and Carson 2010, Yorke et al. 2013). As a result, lianas can have a considerable impact on forest dynamics, tree-species composition, and carbon storage (Laurance et al. 2001, 2014, Schnitzer and Bongers 2002, 2011, Körner 2004).

Here we contrast the dynamics of trees and lianas in fragmented and intact Amazonian forests, using long-term (up to 29-yr) data sets from the world's largest and longest-running experimental study of habitat fragmentation (Lovejoy et al. 1986, Laurance et al. 2002, 2011). The controlled and long-term nature of this experiment, coupled with the large number of replicates and repeated samples available, allow us to draw inferences about the drivers of change in these forests that would otherwise not be possible.

## METHODS

### *Study area*

This study was conducted in fragmented and intact rainforests of the Biological Dynamics of Forest Fragments Project (BDFFP; 2°30' S, 60° W), located 70 km north of Manaus, Brazil. The 69 permanent, 1-ha plots in this study span ~1000 km<sup>2</sup> and range from 60 to 120 m elevation. The study area has been experimentally fragmented but is otherwise nearly free of anthropogenic disturbances such as selective logging, fires, or past agriculture (Laurance et al. 2004, 2005).

The forests of the study area are among the most diverse in the world (averaging ~260 tree species of ≥10 cm diameter at breast height [dbh] per hectare) with a typical canopy height of 37–40 m (S. G. Laurance et al. 2010). The dominant soils in the study area are xanthic ferralsols (Fearnside and Leal Filho 2001), which are heavily weathered and nutrient poor (Beinroth 1975). In this region, clay-rich plateaus are frequently dissected by steep stream gullies, which have higher sand contents and lower concentrations of most soil nutrients (Chauvel et al. 1987). Rainfall ranges

from 1900 to 3500 mm annually with a moderately strong dry season from June to October (Laurance 2001).

The study area includes three large cattle ranges (3000–5000 ha each) containing 11 forest fragments (five of 1 ha, four of 10 ha, two of 100 ha). Expanses of nearby continuous forest serve as experimental controls. In the early–mid 1980s, the fragments were isolated from nearby intact forest by distances of 80–650 m by clearing and often burning the surrounding forest. A key feature was that pre-fragmentation censuses were conducted for trees and many faunal groups, allowing long-term changes in these groups to be assessed far more confidently than in most other fragmentation studies.

The ranches surrounding the BDFFP fragments have been gradually abandoned because of poor soils and low productivity and because many of the government incentives for ranches ended after 1984. Secondary forests (initially dominated by *Vismia* spp. in areas that were cleared and burned or by *Cecropia* spp. in areas that were cleared without fire) proliferated in many formerly cleared areas (Mesquita et al. 2001). To help maintain isolation of the experimental fragments, 100 m-wide strips of regrowth were cleared and burned around each fragment on four or five occasions, most recently in 2013.

### *Data collected*

The 69 permanent plots we studied were established in the early 1980s, with an initial focus on tree-community dynamics and forest-carbon storage (Laurance et al. 1997, 1998, 2006a, b). Within each plot, all trees (≥10 cm dbh) were measured at 1.3 m height or above any buttresses, mapped, and tagged, with sterile or fertile material collected to facilitate species identification. Each plot was recensused at a nominal interval of ~5 years to record any dead, damaged, or newly recruited trees, with the most recent tree census being in 2009. Annualized rates of tree mortality and recruitment were estimated using logarithmic models (Sheil et al. 1995), corrected for variation in census interval (Lewis et al. 2004c).

Liana data in all but three of our plots were initially collected in 1997–1999 (Laurance et al. 2001), with the remaining three plots censused for lianas in early 2001. All plots were resampled, using identical methods, in 2012, for a resampling interval of  $13.5 \pm 0.7$  yr (mean  $\pm$  SD). Within each plot, all lianas (≥2 cm diameter) were counted and measured at 1.3 m height, following established protocols for enumerating liana stems (Putz 1984, Schnitzer et al. 2006). As is typical, no attempt was made to distinguish liana ramets and genets. Liana stems were not individually tagged during the initial survey and thus estimates of liana recruitment and mortality could not be generated. Estimates of liana aboveground dry biomass were derived with an allome-

tric model using liana stem-diameter data ( $D$ ) from many different studies (Schnitzer et al. 2006), as follows:

$$\text{liana biomass} = \exp[-1.484 + 2.657 \ln(D)]. \quad (1)$$

The only exception from established protocols was that, in 1997–1999, we measured the diameter of non-circular liana stems (which constituted just 1.4% of all stems) with a dbh tape, rather than averaging their length and width, as is now recommended (Schnitzer et al. 2006). For the sake of consistency we retained this method in 2012, but found it had little impact on our estimates of liana biomass (using 2012 data, biomass values for each plot calculated using the two methods differed by just 0.5% on average).

Mean slope was determined for each plot with a clinometer, by dividing the plot into 25 subplots (each  $20 \times 20$  m), determining the maximum slope within each subplot, and then averaging these values. In our study area, mean slope is a good proxy for soil texture and nutrient status; the major gradient is between clay-rich soils in flatter areas with higher C, N, cation exchange capacity, and exchangeable bases, and sandy, nutrient-starved soils in steeper sites with greater aluminum toxicity (Laurance et al. 1999, 2001, S. G. Laurance et al. 2010).

#### Data analysis

At the outset, we divided our 69 plots into two categories: edge plots (plot center  $<100$  m from the nearest forest edge) and forest-interior plots (plot center 150–3300 m from the nearest edge). This is because prior analyses have revealed that edge effects are a dominant driver of ecological change in these fragments, at least in the first two to three decades after fragmentation, and are strongest within  $\sim 100$  m of forest edges (Lovejoy et al. 1986, Laurance et al. 1997, 1998, 2000, 2001, 2002, 2006a, b, 2007).

We assessed changes in liana abundance and biomass over time in our plots using paired  $t$  tests. Data were log-transformed prior to analysis if differences between paired samples deviated significantly from normality. Two-sample  $t$  tests, with log-transformed data (to help normalize data and stabilize variances), were used to contrast edge and interior samples.

We tested effects of four possible predictors on liana abundance in 1997–1999, and 2012, and on the annualized rate of change in liana abundance in each plot. Our possible predictors were (1) mean number of trees per plot, (2) mean rate of tree mortality, (3) mean slope of the plot, and (4) a categorization of the plot as edge or interior. To do this, we fitted generalized linear mixed models (GLMM) with negative binomial error distributions and log link functions for liana abundance, and a Gaussian error distribution and identity link function for the rate of change in liana abundance, using the `glmmadmb` function in R's `glmmADMB` package (Bolker et al. 2012). Plots in the study area occur in three relatively discrete blocks, and hence block was included

as a random variable to account for the possible non-independence of samples within the same block. We evaluated potential collinearity between independent variables and found they were not correlated (variance-inflation factors for all variables were  $<3$  [Zuur et al. 2009]). We used an information-theoretic approach for model simplification (Burnham and Anderson 2002), by comparing all possible combinations of independent variables and ranking them by their Akaike information criterion (AIC) scores. We present the results for the single best model selected (lowest AIC score and hence greatest explanatory power).

We also used linear regressions to assess relationships between certain predictor and response variables. We tested for differences in regression slopes using  $Z = (\text{slope}_1 - \text{slope}_2) / (\text{SE}_1^2 + \text{SE}_2^2)^{0.5}$ , where 1 and 2 refer to two different regression slopes and their respective standard errors.

## RESULTS

### Forest dynamics

Long-term forest-dynamics data were available for all but three of our plots. To determine whether forest dynamics changed over time, we contrasted annualized rates of tree mortality and recruitment in forest-edge and forest-interior plots over two intervals, the early–mid 1980s to late 1997 (interval 1), and early 1998 to late 2009 (interval 2).

Forest dynamics increased over time in both forest-interior and edge plots (Fig. 1). In forest interiors, mean tree mortality and recruitment rates were relatively low on average in interval 1 (mean  $\pm$  SD =  $1.33 \pm 0.63$  and  $1.15 \pm 0.31\%$  per yr, respectively) but rose in interval 2 ( $1.46 \pm 0.35$  and  $1.46 \pm 0.52\%$  per yr, respectively). Tree mortality and recruitment both increased over time in two-thirds (22/33) of all interior plots, and declined in the remainder. Mean differences between intervals 1 and 2 were significant for both mortality ( $t = 2.19$ ,  $P = 0.036$ ) and recruitment ( $t = 3.19$ ,  $P = 0.0031$ ; paired  $t$  tests,  $df = 32$ , with log-transformed data).

Relative to forest interiors, tree mortality and recruitment were both markedly elevated in edge plots over the course of the study (mortality  $t = 4.68$ ,  $P < 0.0001$ ; recruitment  $t = 5.52$ ,  $P < 0.0001$ ; paired  $t$  tests,  $df = 32$ , with log-transformed data). This was especially so during interval 1 ( $2.21 \pm 1.02$  and  $2.13 \pm 1.12\%$  per yr, respectively), which corresponds to the first 10–15 years after fragmentation. Tree mortality and recruitment in edge plots declined somewhat in interval 2 ( $1.83 \pm 0.56$  and  $1.98 \pm 0.89\%$  per yr, respectively), but were still significantly higher than those in forest interiors (mortality  $t = 3.27$ ,  $P = 0.0017$ ; recruitment  $t = 3.08$ ,  $P = 0.003$ ; two-sample  $t$  tests,  $df = 64$ , with log-transformed data). In both intervals there was substantial spatial and temporal variation in forest dynamics, largely due to the random nature of windstorms, which had a particularly strong impact on edge plots.

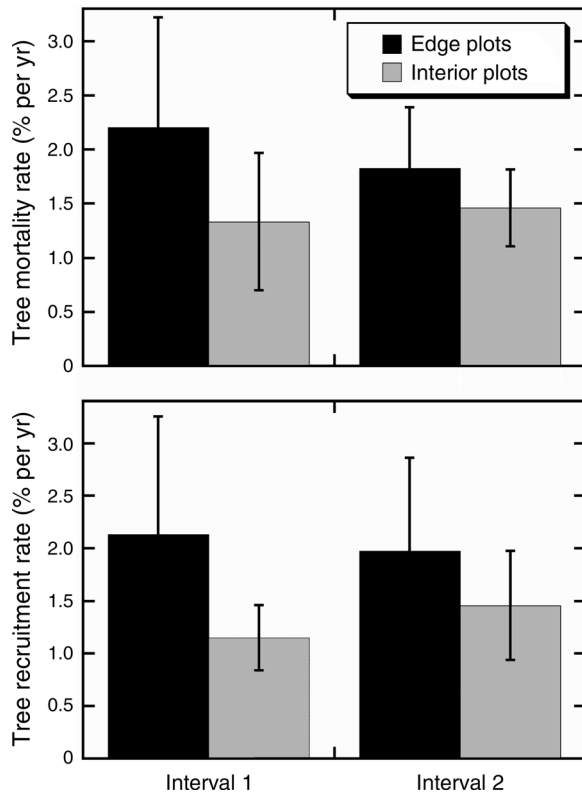


FIG. 1. Annualized rates (mean and SD) of tree mortality and recruitment in 33 1-ha plots near forest edges (plot center <100 m from nearest edge) and 33 1-ha plots in forest interiors (plot center 150–3300 m from nearest edge). Rates are contrasted between interval 1 (early-mid 1980s to late 1997) and interval 2 (early 1998 to late 2009). Data are based on five to eight standardized censuses of trees ( $\geq 10$  cm diameter at breast height) within each plot.

#### *Liana abundance, size distributions, and biomass*

In our 69 plots, we recorded 27 857 lianas in 1997–1999, and 33 895 lianas in 2012. Lianas averaged  $376 \pm 107$  and  $434 \pm 120$  stems/ha (mean  $\pm$  SD) in interior and edge plots, respectively, in 1997–1999. These values rose to  $428 \pm 118$  and  $560 \pm 175$  stems/ha, respectively, in 2012.

During the  $\sim 14$ -yr census interval, lianas increased in abundance in 92% (33/36) of all interior plots and 88% (29/33) of all edge plots (Fig. 2). Annualized rates of increase for liana stems were  $1.00 \pm 0.88\%$  per yr in interiors and  $1.73 \pm 1.23\%$  per yr near edges. Both of these increases were highly statistically significant (interiors  $t = 6.58$ ,  $df = 35$ ,  $P < 0.00001$ ; edges  $t = 8.08$ ,  $df = 32$ ,  $P < 0.00001$ ; paired  $t$  tests with log-transformed liana data).

In terms of liana size distributions (Fig. 3), both interior and edge plots showed a marked increase over time in the number of small (2–3 cm diameter) lianas, which rose by 43% and 53%, respectively, during the study. Larger size-classes of lianas also increased to a degree, especially in edge plots (Fig. 3).

Liana biomass generally rose during the study, but considerably faster near forest edges (averaging  $1.30 \pm 1.39\%$  per yr) than in forest interiors ( $0.32 \pm 1.37\%$  per yr). Mean biomass in interiors increased from  $7.7 \pm 0.2$  Mg/ha in 1997–1999, to  $8.0 \pm 0.2$  Mg/ha in 2012. In edge plots, biomass increased from  $8.1 \pm 0.3$  to  $9.7 \pm 0.3$  Mg/ha over the same interval. These differences were nonsignificant for interior plots ( $t = 1.46$ ,  $df = 35$ ,  $P = 0.15$ ) but highly significant for edge plots ( $t = 5.26$ ,  $df = 32$ ,  $P < 0.0001$ ; paired  $t$  tests with log-transformed biomass data).

In edge plots, the increase over time in liana biomass appeared to result mostly from the increase in larger lianas. The number of large ( $\geq 10$  cm diameter) lianas was a strong and positive predictor of total liana biomass, in both 1997–1999 ( $F_{1,67} = 51.73$ ,  $R^2 = 43.6\%$ ,  $P < 0.0001$ ) and 2012 ( $F_{1,67} = 38.27$ ,  $R^2 = 36.4\%$ ,  $P < 0.0001$ ), across our plot network (linear regressions with log-transformed large-liana data).

#### *Predicting liana abundance*

The GLMM analyses suggested that two variables, the rate of tree mortality and the number of tree stems per plot, were the most effective predictors of liana abundance in 1997–1999 and again in 2012 (Table 1). Both predictors had effects of greater magnitude in the latter census.

The best predictors of the annualized rate of change in liana abundance were tree-mortality and the edge/interior categorical variable (Table 1). Notably, forest edges and interiors exhibited a different relationship between tree mortality and the rate of change in liana abundance (Fig. 4). In edge plots, lianas increased where

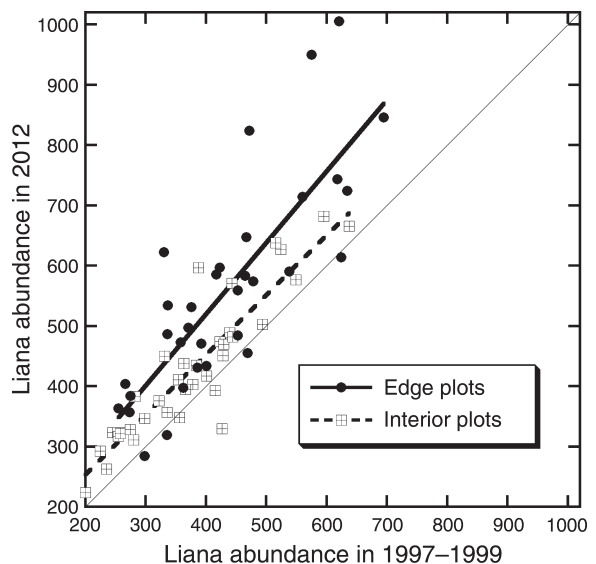


FIG. 2. Comparison of liana abundance (stems  $\geq 2$  cm diameter) between 1997–1999 and 2012 for 69 1-ha plots in fragmented and intact Amazonian forests. The thin solid line shows  $y = x$ , whereas the heavier lines show fitted regressions.

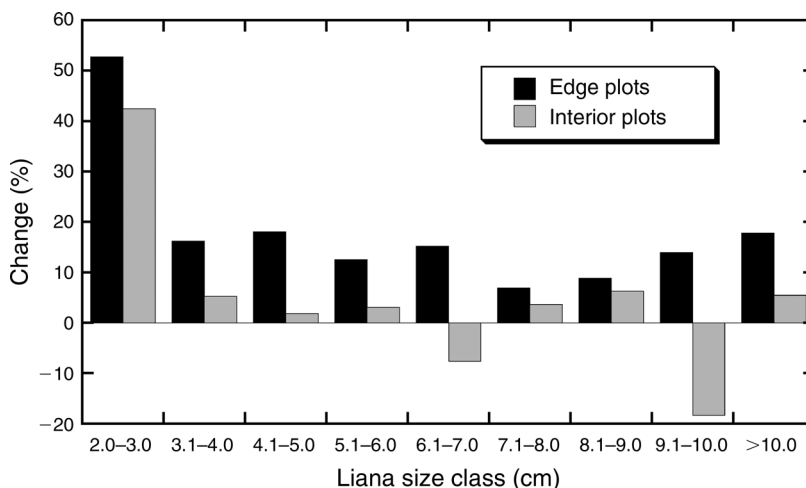


FIG. 3. Relative changes in the frequency of lianas in different size classes in forest-edge and forest-interior plots in central Amazonia between 1997–1999 and 2012. Values are means.

tree mortality was higher ( $F_{1,34} = 18.15$ ,  $R^2 = 36.9\%$ ,  $P = 0.0002$ ), but there was no such relationship in interior plots ( $F_{1,34} = 0.13$ ,  $R^2 = 0.4\%$ ,  $P = 0.72$ ; linear regressions). The slopes of the fitted regression lines for edge and interior plots differed significantly ( $Z = 3.041$ ,  $P = 0.0024$ ).

#### DISCUSSION

##### *Changes in intact forests*

When our large-scale forest fragmentation experiment was initiated in 1979, two types of experimental controls were established as ecological baselines: pre-fragmentation samples of all plots, and long-term monitoring of plots in nearby intact forest (Lovejoy et al. 1986, Bierregaard et al. 1992). At that time, it was expected

that the intact-forest controls would either vary randomly or respond to occasional vicissitudes such as droughts, but would be largely stable overall. They have not. Rather, the intact forests in our study area have changed in several largely concerted ways. Hence, the controls have not behaved as expected, leaving one scrambling to interpret the results of the fragmentation experiment at the heart of this investigation.

How have the intact forests changed? To date, we have found that (1) forest dynamics (tree mortality and recruitment) have accelerated over time (Fig. 1; Laurance et al. 2004, S. G. Laurance et al. 2009); (2) tree-community composition has shifted, generally in favor of faster-growing canopy trees and against shade-tolerant subcanopy trees (Laurance et al. 2004, 2005); (3) growth rates have increased for the large majority

TABLE 1. The most parsimonious predictors of liana abundance (stems/ha) in 1997–1999 and 2012, as well as the annualized rate of change in lianas, within 66 1-ha plots in fragmented and intact Amazonian forest.

Predictor	Estimate	SE	Z	P
Liana abundance in 1997–1999				
Intercept	5.995	0.032	187.90	<0.00001
Number of tree stems	0.077	0.034	2.25	0.024
Tree mortality rate	0.058	0.034	1.69	0.092
Liana abundance in 2012				
Intercept	6.183	0.036	170.97	<0.00001
Tree mortality rate	0.129	0.032	4.02	<0.00001
Number of tree stems	0.096	0.035	2.75	0.0059
Annual change in liana abundance				
Intercept	1.213	0.211	5.76	<0.00001
Tree mortality rate	0.453	0.131	3.46	0.00053
Forest edge vs. interior†	0.365	0.268	1.36	0.173

Notes: Generalized linear mixed-effects models were used with AIC-informed selection of the most parsimonious predictors. Experimental block was included as a random variable. The effect size of each predictor is proportional to the absolute value of its estimate, with positive values indicating a positive slope. Three plots that were initially sampled for lianas in 2001 are excluded from these analyses. Tree mortality rate data were  $\log_{10}$ -transformed.

† Categorical variable.



(84%) of tree genera (Laurance et al. 2004); (4) aboveground forest biomass has increased over time (although tree-stem numbers have not changed significantly; S. G. Laurance et al. 2009); and (5) lianas have increased markedly in abundance (Fig. 2; Laurance et al. 2014).

Why are the intact forests changing? The causes of such changes are incompletely understood (Lewis et al. 2004a, 2009a) and often controversial (Clark 2004, Fearnside 2004). Nonetheless, the trends we detected appear broadly consistent with those observed elsewhere in many Amazonian (Phillips and Gentry 1994, Phillips et al. 1998, 2002, Baker et al. 2004, Lewis et al. 2004b, Schnitzer and Bongers 2011) and African (Lewis et al. 2009b) tropical forests. The trends are also consistent with ecological patterns expected from rising forest productivity—including faster plant growth, increasing forest biomass, intensifying competition leading to greater plant mortality and turnover, and increasing abundances of plant species that can attain high growth rates or that favor dynamic forests (Laurance et al. 2004, Lewis et al. 2004b, 2009a).

The most frequently invoked driver of rising tropical forest productivity is CO<sub>2</sub> fertilization (e.g., Lewis et al. 2009a), because many plants show faster growth under enriched CO<sub>2</sub> (Oberbauer et al. 1985, Granados and Körner 2002, Körner 2004) and because atmospheric CO<sub>2</sub> levels have risen rapidly, especially in recent decades. This view is supported by compelling evidence of a large carbon sink in the biosphere (Ballantyne et al. 2013), a substantial part of which appears to be on land (Sarmiento et al. 2010) and in the tropics (Lewis et al. 2009a, Huntingford et al. 2013).

Other explanations for the rising productivity, however, are not implausible. For instance, droughts can influence forest dynamics and composition and might be increasing in parts of the Amazon (Lewis et al. 2011, Butt et al. 2012, Fu et al. 2013). Additionally, multi-decadal shifts in solar radiation or cloudiness could potentially increase forest productivity, although evidence for such shifts in the tropics is limited (Lewis et al. 2009a). Recovery from past disturbance has also been hypothesized to underlay changes at some tropical forest sites, but there is no evidence of widespread disturbance in our study area (Laurance et al. 2004, 2005) aside from charcoal fragments that are at least four centuries old (Bassini and Becker 1990, Fearnside and Leal Filho 2001), possibly indicating major fires during past mega-El Niño events (Meggers 1994). Whatever the reason, or reasons, it is apparent that the intact forests in our study area are changing in a number of ways.

#### *Changes in forest fragments*

The concerted trends in our control sites suggest that a nuanced view is needed to interpret the results of our forest fragmentation experiment. The observed trends in fragments may well result from a combination of local-

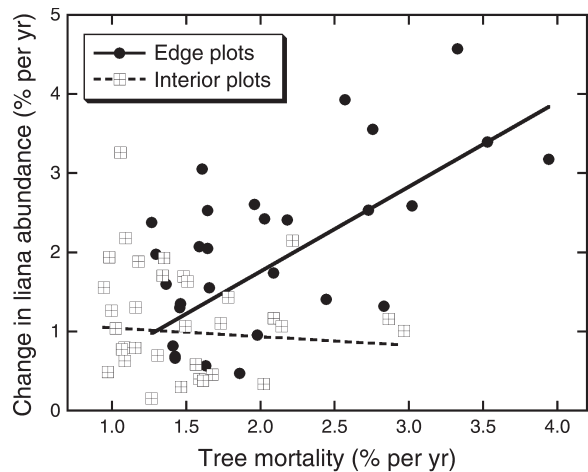


FIG. 4. Relationship between annual tree mortality and the annual change in liana abundance in 69 1-ha plots in fragmented and intact Amazonian forests. Slopes of the fitted regression lines differed significantly ( $Z = 3.041$ ,  $P = 0.0024$ ). Values shown are means. See *Methods: Data analysis* for calculation of  $Z$ .

scale fragmentation effects and one or more phenomena presumptively operating at global or regional scales.

In simplest terms, one might assume that the fragmentation and larger-scale drivers operate additively. If this were the case, then one could subtract the mean observed changes in intact forest from the mean observed changes in fragments, in order to estimate the actual magnitude of fragmentation effects. This would lead one to conclude that, on average, about 74% of the elevated tree mortality, 59% of the elevated tree recruitment, and 42% of the elevated liana abundance in forest fragments resulted from fragmentation and edge effects, with the remaining changes caused by larger-scale drivers. Despite the coarseness of this approach, it is in fact about the best one can do to estimate the relative magnitude of these apparent effects.

In reality, however, fragmentation and larger-scale drivers might interact in more complex or synergistic ways. For instance, the mean rate of tree mortality was initially very high near forest edges, but then attenuated somewhat 10–15 years after fragmentation (Fig. 1). In forest interiors, however, mortality rates were lower on average but then rose significantly over time. Presumably, the dynamics of tree mortality in fragments reflected an interaction between these two forces: a modest but long-term increase in tree mortality that affected the entire study area and a strong but attenuating pattern of tree mortality near forest edges. The fall-off in mortality near edges could have occurred for three reasons. First, the most vulnerable trees near edges tend to die quickly (Laurance et al. 1998). Second, newly created edges are initially permeable to wind and microclimate stresses that can kill trees, but become more “closed” over time by proliferating vines and lateral branch growth (Laurance et al. 2002, 2007,

D'Angelo et al. 2004). Finally, in the BDFFP landscape, relatively tall (up to 20 m height) secondary forests regenerated over time near many fragments, buffering edge effects and thereby reducing tree mortality (Mesquita et al. 1999).

Lianas also seemed to show complex dynamics across the landscape. As a group, lianas are known to respond positively to forest disturbance (Webb 1958, Putz 1984) and drought (Schnitzer 2005, Cai et al. 2009), and benefit from enriched CO<sub>2</sub> (Granados and Körner 2002, Hättenschwiler and Körner 2003). In our study area, lianas became more abundant over time in edge plots with high tree mortality, but there was quite a different relationship in forest interiors (Fig. 4). This difference suggests that the changes in liana abundance in intact forest might have had a different cause than those in fragments: one not directly related to increasing forest dynamics, such as, for instance, rising CO<sub>2</sub> levels (there is no evidence that droughts increased during our study; Laurance et al. 2014). In fragments, however, a combination of elevated tree mortality (Fig. 1), increased light and desiccation near forest edges (Kapos 1989), and a large-scale driver such as elevated CO<sub>2</sub> might have collectively favored lianas.

In yet other cases, the putative large-scale driver might tend to counter trends in forest fragments. For instance, the accelerated tree growth rates and increasing tree biomass observed in intact forests (Laurance et al. 2004, S. G. Laurance et al. 2009) would presumably oppose (to a limited degree) the strong "biomass collapse" driven by elevated tree mortality in fragments (Laurance et al. 1997, 2000).

When forest fragmentation and the presumptive large-scale driver operate in concert, as is apparently the case for forest dynamics and lianas, then their ecological effects might be magnified. As detailed elsewhere, increasing forest dynamics and proliferating lianas can have a variety of ecological consequences, changing forest structure, altering the dynamics of forest carbon stocks, and driving shifts in the species composition of plant communities and dependent fauna (e.g., Laurance et al. 1997, 2002, 2006a, 2011, Körner 2004, Schnitzer and Bongers 2011).

### Summary

Forests in our study area and many other locations in the Amazon are evidently experiencing concerted large-scale changes, including increasing tree growth rates, faster tree mortality and recruitment rates, increasing forest biomass, shifts in tree-community composition, and increasing liana abundances, that are broadly consistent with the expected effects of rising forest productivity. Plant fertilization from rising atmospheric CO<sub>2</sub> concentrations is the most obvious, but not only, potential driver of these changes.

Interpreting the findings of the Biological Dynamics of Forest Fragments Project (BDFFP) requires disentangling the apparent effects of rising forest productivity

from those of the fragmentation experiment itself. In the simplest terms, and assuming such effects are additive, increasing productivity might account for roughly 25–60% of the observed increases in forest dynamism and liana abundance documented here, depending upon the specific phenomenon under consideration.

It is far from apparent, however, that accelerating productivity and fragmentation effects would interact in a simple, additive manner. Fragmented landscapes are dynamic, with strong temporal and spatial changes in fragments as a result of changing matrix and edge vegetation and external vicissitudes such as windstorms (Laurance 2002). At a minimum, such dynamics could complicate the interactions of fragmentation with larger-scale drivers. More generally, if fragment dynamics are also being influenced by large-scale environmental drivers, then it could be very challenging to predict the long-term consequences of habitat fragmentation.

Given the potential ubiquity of large-scale anthropogenic influences today, it seems naïve to assume important ecological and land-use experiments are free of such effects. At the BDFFP, we had a fighting chance to discern such influences because of the highly replicated and long-term nature of our study, and its large spatial scale. Elsewhere, researchers should be aware of the potentially confounding effects of large-scale environmental changes, and if possible should design careful experiments to identify and measure their effects. In these settings, there will rarely be true experimental controls because, by their very nature, large-scale changes are occurring virtually everywhere. It is not inconceivable that such drivers are affecting most terrestrial ecosystems on Earth, whether impacted by anthropogenic land-use changes or not.

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