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Contrasting Demographic Structure of Short- and Long-lived Pioneer Tree Species on Amazonian Forest Edges

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ABSTRACT

Although tropical forests have been rapidly converted into human-modified landscapes, tree species response to forest edges remains poorly examined. In this study, we addressed four pioneer tree species to document demographic shifts experienced by this key ecological group and make inferences about pioneer response to forest edges. All individuals with dbh $\geq$ 1 cm of two short-lived (*Bellucia grossularioides* and *Cecropia sciadophylla*) and two long-lived species (*Goupia glabra* and *Laetia procera*) were sampled in 20 1-ha forest edge plots and 20 1-ha forest interior plots in Oiapoque and Manaus, Northeast and Central Amazon, respectively. As expected, pioneer stem density with dbh $\geq$ 1 cm increased by around 10–17-fold along forest edges regardless of species, lifespan, and study site. Edge populations of long-lived pioneers presented 84–94 percent of their individuals in sapling/subadult size classes, whereas edge populations of short-lived pioneers showed 56–97 percent of their individuals in adult size classes. These demographic biases were associated with negative and positive net adult recruitment of long- and short-lived pioneers, respectively. Our population-level analyses support three general statements: (1) native pioneer tree species proliferate along forest edges (*i.e.,* increased density), at least in terms of non-reproductive individuals; (2) pioneer response to edge establishment is not homogeneous as species differ in terms of demographic structure and net adult recruitment; and (3) some pioneer species, particularly long-lived ones, may experience population decline due to adult sensitivity to edge-affected habitats.

Key words: *Bellucia grossularioides*; *Cecropia sciadophylla*; edge effects; *Goupia glabra*; habitat fragmentation; *Laetia procera*; plant demography.

Habitat loss and fragmentation represent a key force on the ongoing global crisis of biodiversity and associated ecosystem services (Laurance & Peres 2006). About 710,000 km^2 (17%) of the Amazon Basin had been deforested by 2006 (Vieira *et al.* 2008), especially in the 'arc of deforestation' on the southern and eastern boundaries. New deforestation frontiers have arisen in Central and Northern Amazonia as well, resulting in 'archipelagos' of small forest fragments and the creation of 70,000 km of new forest edges every year (Fearnside 2005, Silva *et al.* 2005, Broadbent *et al.* 2008). These changes in landscape configuration negatively affect the remaining biota due to area, isolation, and matrix effects (Ewers & Didham 2006), but edge effects persist as the main drivers of ecological changes experienced by forest fragments (Laurance *et al.* 2011).

Edge effects consist of abiotic and biotic processes operating along forest edges, which result in distorted tree assemblages. Recent evidence from an aging (>200 yr-old) and hyper-fragmented landscape in the Atlantic forest of Northeast Brazil suggests that edge effects represent the main force for driving forest fragments or edge-affected habitats toward early-successional systems (Santos *et al.* 2008, 2010; Tabarelli *et al.* 2008, Lopes *et al.* 2009, see also Pütz *et al.* 2011, but see Borouncle & Finegan 2011). The striking biomass collapse, floristic simplification, and functional impoverishment observed in recently (<40 yr-old) isolated Amazonian forest fragments indicate that such trajectory may be operational in the Amazon as well (Laurance *et al.* 2011 and references therein). Our current understanding on the demography of individual tropical tree species along forest edges, however, remains insufficient to make accurate predictions about population persistence and potential successional trajectory experienced by such altered habitats (but see Brum *et al.* 2008 for the tree palm *Oenocarpus bacaba).* In the context of demographic responses to edge effects, several studies have demonstrated that populations of the perennial herb *Heliconia acuminata* are skewed toward smaller size classes in Amazonian forest fragments (*e.g.,* Bruna 2002, Bruna & Kress 2002, Bruna & Oli 2005), possibly due to chronic reduction in plant growth and inflorescence production in forest fragments (Gagnon *et al.* 2011).

It is well known that seedlings, saplings, and adults of some pioneer tree species are able to dominate forest edges (Sizer & Tanner 1999, Laurance *et al.* 2006, Michalski *et al.* 2007, Santos *et al.* 2008), but whether short- and long-lived pioneer species respond similarly in terms of demographic structure is an open question. Overall, short-lived pioneers (*i.e.,* lifespan <50 yr) have their demography completely associated with forest gaps, but their smaller adults usually thrive along forest edges (Tabarelli *et al.* 2010a, Laurance *et al.* 2011), indicating recent canopy

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disturbance (Whitmore 1989). Long-lived pioneers (*i.e.,* lifespan >50 yr) are also gap-dependent, but their taller, emergent adults generally persist in later successional stages by attaining the upper strata before canopy closure. Such large trees are relicts of past forest disturbance (Clark & Clark 1996) and usually vanish from forest edges due to increased wind turbulence and habitat desiccation (D'Ângelo *et al.* 2004, Laurance & Curran 2008). Based on such regeneration strategies, it is reasonable to expect that after some decades of edge creation, differences in adult recruitment and mortality between short- and long-lived pioneers may result in distinct demographic structures, affecting their relative contribution to forest structure, composition, and functioning along forest edges.

In this study, we sampled four pioneer tree species (two short- and two long-lived) across edge and forest interior plots of two Amazonian sites to document demographic shifts experienced by this key ecological group and make inferences about pioneer response to forest edges. We expected to find a proliferation of pioneer species across edge plots (*i.e.,* a positive response to edge establishment), with edge populations of short-lived species supporting a large number of adults (no adult recruitment bottlenecks), whereas those of long-lived species being mostly represented by saplings/subadults due to negative net adult recruitment. First, we documented cross-habitat shifts on stem density (edge vs. interior plots) and described size-distribution of stems (hereafter demographic structure) considering all species, habitats, and sites. Second, we offered estimates of adult recruitment and mortality over 23–27 yr for four species in one of the study sites. Finally, we explored the generality of our findings and provide some insights regarding pioneer demographic responses, species persistence, and the successional trajectory experienced by edge-affected habitats in human-modified landscapes.

METHODS

STUDY SITES.—The study was conducted near the cities of Oiapoque and Manaus, Northeast and Central Amazon (Fig. S1A). In Northeast Amazon, the study site refers to a private cattle ranch located 40 km south of Oiapoque at 100 m asl (3° 33′ 44″ N, 51° 47′ 22″ W; Fig. S1B). The study site is located in the rain forest eco-region (*i.e., terra firme* forest) in a sub-region called 'Superfície Dissecada Guianense'. Annual rainfall averages 2500 mm, with pronounced dry season from September to November (Souza & Cunha 2010). Average annual temperature is 26.5°C and soils vary with topography from red-yellow distrophic latosoil to red-yellow argisoil.

In Central Amazon, the study area is the 1000-km^2 experimentally fragmented landscape of the Biological Dynamics of Forest Fragments Project (BDFFP), located 80 km north of Manaus at 100–150 m asl (2° 26′ 00″ S, 59° 52′ 25″ W; Fig. S1C). The mean annual precipitation is 2200 mm with a pronounced dry season from June to September. Average temperature is 26.7°C and the predominant soil type is clay distrophic yellow latosoil (Laurance *et al.* 1999). *Terra firme* tropical rain forests account for most of the vegetation cover of the study area. Forest canopy is 30–37 m tall, with some emergent trees reaching 55 m. Tree species richness ($\geq$ 10 cm diameter at breast height [dbh]) may exceed 280 species/ha (Oliveira & Mori 1999).

Landscape matrix differs between the study sites. In Oiapoque, pastures were established in late 1990s and have been maintained through annual burnings. In Manaus, pastures were opened in the 1980s and abandoned in the early 1990s. Fire was used in some BDFFP areas and not used in others, resulting in secondary forest patches dominated by *Vismia* and *Cecropia* species, respectively (Mesquita *et al.* 1999, Williamson & Mesquita 2001). The attributes of surrounding matrix have been recognized to affect tree recruitment along forest edges and may confound the demographic responses of pioneer trees to edge proximity/effects (Nascimento *et al.* 2006).

PLANT SURVEYS.—In this study, we sampled four phylogenetically unrelated pioneer species – two short-lived (*Bellucia grossularioides* and *Cecropia sciadophylla*) and two long-lived (*Goupia glabra* and *Laetia procera*). These four taxa refer to light-demanding, fast-growing tree species with continuous or annual reproduction, and high ability to rapidly respond to human changes in the landscape configuration (Laurance *et al.* 2006, Bentos *et al.* 2008, Zalamea *et al.* 2008, 2011); *i.e.,* they are typical early colonizers in the Amazon Basin (Table 1). Between September and December 2007, we established 20 1-ha plots (100 × 100 m) in a vast tract of continuous forest in Oiapoque: ten at 0 m from the edge (edge plots) and ten in core areas (interior plots) 1000 m away from the nearest edge. The first edge plot was randomly selected and the others were located every 300 m along the forest edge. No edge plot was simultaneously exposed to two edges and interior plots were disposed in pairs with edge ones. In Manaus, a long-term study of vegetation dynamics has been conducted in forest fragments and continuous forests since early 1980s. About 65,000 trees (dbh $\geq$ 10 cm) have been periodically monitored in 66 1-ha permanent plots distributed across 1-ha, 10-ha, and 100-ha forest fragments and several continuous forests (Rankin-de-Merona *et al.* 1990, Laurance *et al.* 1998). Tree mortality, recruitment, and growth have been recorded every 4–6 yr. More recently, stems sizing 1–9.9 cm dbh started to be included in plant inventories within each 1-ha plot. For this study, we randomly selected 20 of the 66 BDFFP plots: ten edge plots and ten interior plots.

In each of the 40 1-ha plots, all individuals with dbh $\geq$ 1 cm of the four selected species were classified into four size classes according to their dbh: I (1 to <2 cm), II (2 to <10 cm), III (10 to <20 cm), and IV ($\geq$ 20 cm). The proportion of individuals in each size class was used to characterize the demographic structure of these edge populations. During the latest BDFFP vegetation census, the short-lived *B. grossularioides* was not present in any plot and the long-lived *L. procera* had not been systematically sampled for saplings and subadults (1.0–9.9 cm dbh). Thus, we excluded these species from the demographic structure analyses for Manaus. Finally, we used the BDFFP data to estimate net adult recruitment along forest edges for each species, calculated by the number of trees (dbh $\geq$ 10 cm) present in the last census after 23–27 yr of

TABLE 1. *Pioneer tree species studied, their family, lifespan, minimum dbh (cm) for flowering, reproductive frequency, and known pollinators and seed dispersers. Modified from Bentos* et al. *2008.*

	Bellucia glossularioides	*Cecropia sciadophylla*	*Goupia glabra*	*Laetia procera*
Family	Melastomataceae	Urticaceae	Celastraceae	Salicaceae
Lifespan	Short-lived	Short-lived	Long-lived	Long-lived
Maximum height (m)	20–25	30	40	35
Minimum reproduction dbh (cm)	7.8	4.8	8.6	15.7
Reproduction frequency	Continuously	Annually	Continuously	Annually
Pollinator	Bees	Bats	Bees	Bees
Disperser	Birds, monkeys	Birds, bats, monkeys	Birds	Birds, monkeys

fragmentation ('final number of trees') minus the number of trees established before fragmentation ('initial number of trees'). Unfortunately, we were not able to examine net sapling recruitment because they were sampled only once, but we are aware that the absence of dynamic data on sapling mortality and recruitment (still rare in the literature) limits the conclusions that could be drawn from our findings.

Statistical analyses.—All analyses were performed separately for Oiapoque and Manaus sites. To examine whether or not plant density differed between edge and interior plots, we ran a generalized linear mixed model with habitat, species, and their interaction as fixed factors and plot nested within habitat as a random factor. The number of individuals per 1-ha was set as a dependent variable after log (x + 1) transformation. Random factor was used to increase the explanatory power of the model and to estimate the magnitude of the unexplained variance attributed to differences among plots (a measure of spatial variation in plant density). We used residual maximum likelihood method (REML) to separate variances of random and fixed effects (Grafen & Hails 2002) and Tukey–Kramer HSD (honestly significant difference) tests to compare differences among treatments.

On the edges of both Oiapoque and Manaus sites, population size at the 1-ha basis was too small to provide a reasonable representation of the demographic structure at this spatial scale (median plant density per species was lower than 15 plants per hectare in both sites). Thus, we pooled data from all ten edge plots, classified individuals into the four size classes (I, II, III, and IV), and then used likelihood ratio Chi-square tests to compare the demographic structure among species. For Oiapoque, the proportion of individuals in each size classes was compared not only among the four species but also between pairs of species with similar lifespan (*i.e., Bellucia* vs. *Cecropia* and *Goupia* vs. *Laetia*). Finally, we used one-way analysis of variance to compare the net adult recruitment among species after log (x + 1) transformation of initial and final number of trees. All analyses were performed in JMP 7 (SAS Institute Inc., Cary, NC, USA). We report mean and standard errors for untransformed data.

RESULTS

Edge effects on stem density.—We recorded a total of 643 individuals ≥ 1 cm dbh in the 20 Oiapoque plots: 74 of *B. grossularioides*, 195 of *C. sciadophylla*, 266 of *G. glabra,* and 108 of *L. procera.* As expected, there was a very strong effect of habitat type on the density of all species considered ($F_{1,18} = 44.1$; $P < 0.0001$). Plant density was on average 17-fold greater in edge than in interior plots (60.8 ind/ha vs. 3.5 ind/ha; Fig. 1A), despite species identity ($F_{3,54} = 2.3$; $P = 0.085$; Fig. 1B). In Manaus, we recorded a total of 283 individuals: 157 of *C. sciadophylla* and 126 of *G. glabra.* As in Oiapoque, habitat type affected significantly plant density ($F_{1,18} = 8.1$; $P < 0.01$), which was on average 10-fold greater in edge than in interior plots (25.9 ind/ha vs. 2.4 ind/ha; Fig. 1C), irrespective of species identity ($F_{1,18} = 1.9$; $P = 0.185$; Fig. 1D).

Demographic structure of edge populations.—In Oiapoque, the demographic structure of edge populations varied not only among species differing in lifespan ($\chi^2 = 410.5$; df = 9; $P < 0.0001$) but also between species with similar lifespan (short-lived species $\chi^2 = 53.1$; df = 3; $P < 0.0001$; long-lived species $\chi^2 = 35.8$; df = 3; $P < 0.0001$). Despite these differences, 94 and 84 percent of the total individuals of the long-lived *G. glabra* and *L. procera* were <10 cm (classes I and II), respectively, whereas 80 and 56 percent of the individuals belonging to the short-lived *C. sciadophylla* and *B. glossularioides* were ≥ 10 cm (classes III and IV) (Fig. 2A). A similar trend was observed in the edge populations of Manaus. About 87 percent of the individuals of the long-lived *G. glabra* were assigned to classes I and II, whereas 97 percent of the individuals of the short-lived *C. sciadophylla* were classified into categories III and IV ($\chi^2 = 220.3$; df = 3; $P < 0.0001$) (Fig. 2B).

Net adult recruitment.—At the edge plots of Manaus, net adult recruitment differed significantly among species ($F_{3,36} = 4.6$; $P = 0.0079$), but it was remarkably greater in *C. sciadophylla* as compared with the other species (Tukey–Kramer HSD test, $P < 0.05$) (Fig. 3). After 23–27 yr of fragmentation, all *B. grossularioides* adults established before fragmentation died ($N = 3$) and were not replaced by any other adults, resulting in the collapse of this short-lived pioneer along the edges. On the other hand, the two *C. sciadophylla* adults established before fragmentation died, but were replaced by 150 new adults (113 of them in only one plot [see the size of error bar in Fig. 3]). According to our initial prediction, the long-lived *G. glabra* and *L. procera* exhibited a negative net recruitment of adults along forest edges. More specifically, there were 15 *G. glabra* adults established before fragmentation and only ten remained after 23–27 yr of fragmentation.

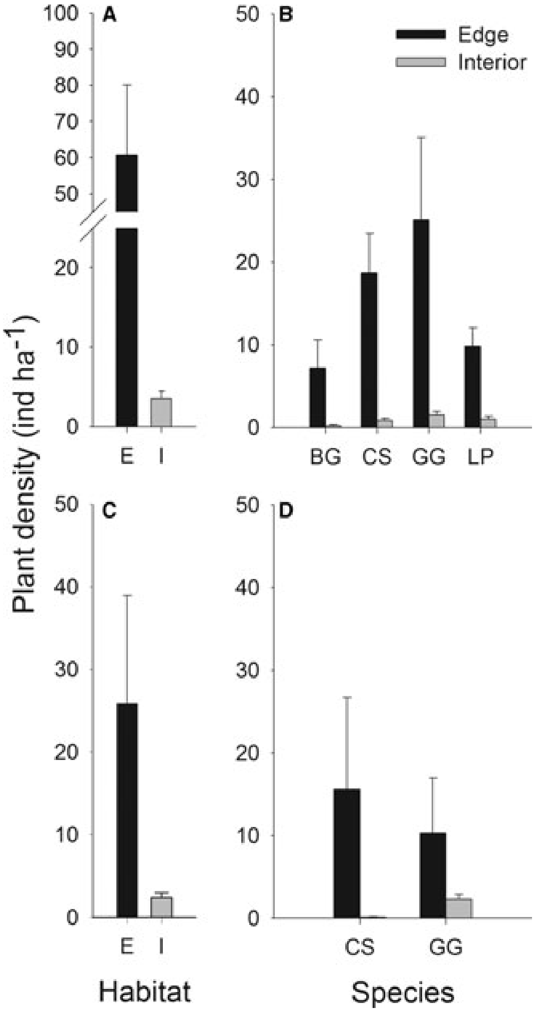

FIGURE 1. Plant density (mean ± SE) of *Bellucia grossularioides* (BG), *Cecropia sciadophylla* (CS), *Goupia glabra* (GG), and *Laetia procera* (LP) in ten edge and ten interior 1-ha plots at Oiapoque, Northeast Amazonia (A, B), and Manaus, Central Amazonia (C, D). In figures A and C, letters E and I represent edge and interior, respectively.

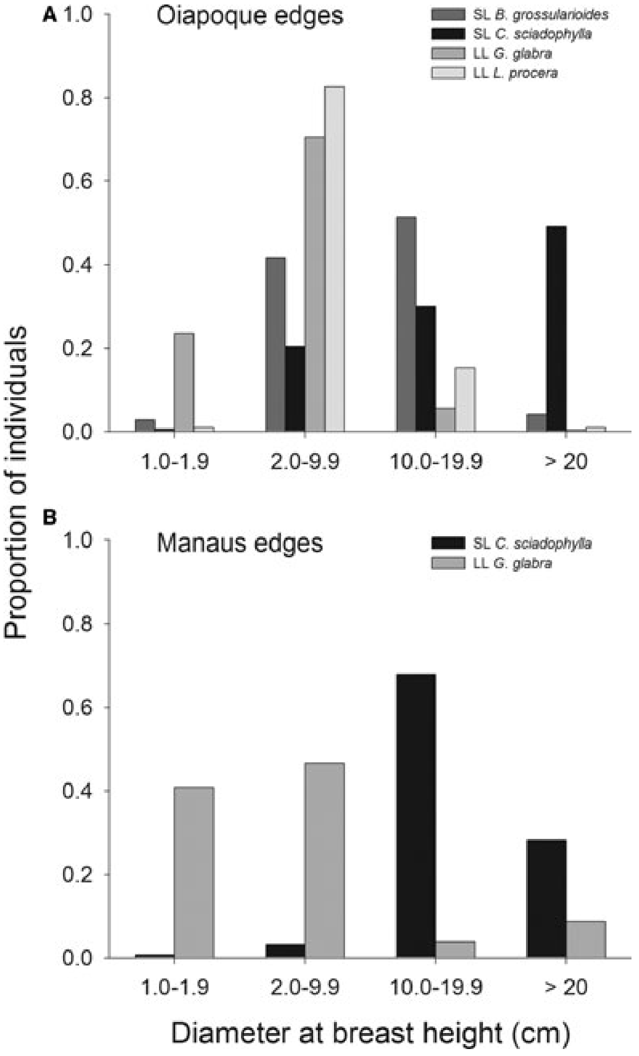

FIGURE 2. Demographic structure of short- and long-lived pioneer tree species along forest edges in (A) Oiapoque (Northeast Amazonia) and (B) Manaus (Central Amazonia), Brazil. Population size in Oiapaque was 72, 187, 251, and 98 for *Bellucia grossularioides, Cecropia sciadophylla, Goupia glabra,* and *Laetia procera*, respectively. In Manaus it was 153 for *C. sciadophylla* and 103 for *G. glabra*. SL, short-lived; LL, long-lived.

Similarly, *L. procera* was represented by six individuals before fragmentation and by four, three decades later.

DISCUSSION

Our population-level analyses, although based on a limited number of species, support three general statements: (1) native pioneer tree species proliferate along forest edges (*i.e.,* increased density), at least in terms of non-reproductive individuals; (2) pioneer response to edge establishment is not homogeneous as species differ in terms of demographic structure and net adult recruitment; and (3) some pioneer species, particularly long-lived ones, may experience population decline due to adult sensitivity to forest edges. Briefly, stem density of pioneers increased by around 10–17-fold along forest edges regardless of species, lifespan, and study site. Edge populations of long-lived pioneers, however, presented most of their individuals (84–94%, 82–235 individuals) in sapling/subadult size classes, whereas edge populations of short-lived pioneers showed most of their individuals (56–97%, 40–148 individuals) in adult size classes, corroborating our initial prediction. These demographic patterns were consistent with a positive net adult recruitment experienced by the short-lived *C. sciadophylla*, whereas both long-lived pioneer species exhibited a negative recruitment of adults.

Proliferation of pioneer species on forest edges and small forest fragments (*i.e.,* edge-affected habitats) is not a novelty in the Amazon (*e.g.,* Laurance *et al.* 2006, Michalski *et al.* 2007) and

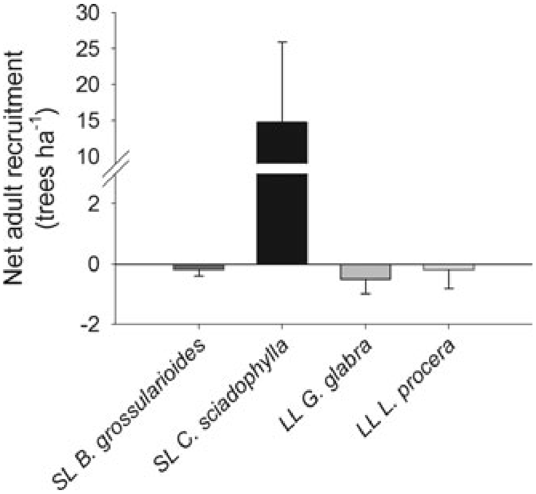

FIGURE 3. Net adult recruitment (mean ± SE) of *Bellucia grossularioides*, *Cecropia sciadophylla*, *Goupia glabra,* and *Laetia procera* along forest edges after 23–27 yr of fragmentation near Manaus, Central Amazonia, Brazil. SL, short-lived; LL, long-lived.

Atlantic forest (Santos *et al.* 2008, Tabarelli *et al.* 2010b). At Manaus, forest regeneration following clear-cutting and cattle raising (*i.e.,* abandoned pastures) has originated second-growth stands dominated by either *Cecropia* or *Vismia* species (Mesquita *et al.* 1999, Williamson & Mesquita 2001). This change in landscape matrix differentially affected the recruitment of certain pioneer tree species on abutting forest edges (Nascimento *et al.* 2006). *C. sciadophylla*, in particular, accounted for nearly 50 percent of all pioneer trees in *Cecropia*-surrounded fragments, indicating that some pioneers species are proliferating across a wide range of habitats in human-modified landscapes (Tabarelli *et al.* 2010b, Laurance *et al.* 2011). More than a landscape-level phenomenon, such proliferation is apparently operating at multiple spatial scales. In the Atlantic forest of Northeast Brazil, where forest conversion to agriculture dates back to 18th century and forest edges account for most of the remaining vegetation (Ranta *et al.* 1998, Ribeiro *et al.* 2009), native pioneer tree species have driven remaining forest patches to biotic homogenization at regional level (Lôbo *et al.* 2011). Compared with Atlantic forest landscapes, our Amazonian study sites are much younger (<40 yr-old) and still embedded within less fragmented and deforested landscapes, but edge-affected habitats are apparently following the same successional trajectory owing to the proliferation of pioneer species. In fact, Amazonian findings reinforce the notion that edge-induced microclimatic changes can maintain suitable conditions for pioneer recruitment and cycles of pioneer self-replacement (*i.e.,* multi- rather than single regeneration pioneer assemblages), leading edge-affected habitats toward early-successional systems; *i.e.,* a permanent shift in the successional trajectory experienced by edge-affected habitats (Tabarelli *et al.* 2008, Pütz *et al.* 2011).

Overall, our results indicate that pioneer species may benefit from edge-affected habitats, at least in terms of juvenile abundance, but they differ in their response as indicated by the demographic structures and patterns of adult recruitment/mortality we observed. In fact, the short- and long-lived pioneer tree species analyzed share several life-history traits, such as rapid growth, dependence on generalist vectors of pollination and seed dispersal, and copious seed production, which have been considered to favor their establishment/proliferation in human-dominated Neotropical landscapes (Tabarelli *et al.* 2008, Lopes *et al.* 2009). Laurance *et al.* (2006), for instance, showed a strong positive relationship between growth rate and adult net recruitment by using a subset of 30 successional tree species established along forest edges in the Manaus site, suggesting that growth rate is a good predictor for the early establishment success of pioneer tree species in recently fragmented forests. Both long-lived species examined here, however, as well as one short-lived in a particular site, exhibited edge populations that clearly deviated toward non-reproductive individuals with a negative adult net recruitment. One potential process explains this recruitment bottleneck of large trees in edge-affected habitats: the pervasive wind turbulence in the upper strata of the forest, which increases mortality of large trees by uprooting and physiological stress (Ennos 1997, Laurance *et al.* 2000, D'Ângelo *et al.* 2004). In addition, this mechanic force also suppresses the recruitment of new large individuals, which continue inhabiting the canopy stratum, but exhibit a depressed height/dbh stem ratio (Oliveira *et al.* 2008). This abiotic filtering may prevent saplings and subadults of long-lived pioneers from attaining the emergent layer of the forest and becoming adults (Oliveira *et al.* 2008, Paula *et al.* 2011), resulting in the negative net adult recruitment and the demographic bias toward smaller size classes we documented here. In the long run, increased recruitment of juveniles triggered by edge creation may not compensated for negative net adult recruitment, making the persistence of long-lived pioneers in edge-affected habitats dependent on source habitat as proposed elsewhere (Oliveira *et al.* 2008).

Unlike long-lived pioneers and their more robust adults, individuals of short-lived pioneers do not need to attain the emergent stratum of the forest to properly reproduce (Whitmore 1989). Instead, saplings and subadults of short-lived pioneers can take advantage of the increased number of canopy gaps along forest edges to rapidly grow, achieve maturity, and leave descendents (Kapos *et al.* 1993, Laurance *et al.* 2006). Once these short-lived trees age and start to die, canopy disturbance increases again, leaving light available for seed germination and seedling recruitment along forest edges, including conspecifics (Melo & Tabarelli 2003). This dynamic, however, may be spatially variable as it is affected by deterministic and stochastic processes that jointly determine local species abundance (*e.g.,* dispersal and recruitment limitation, Hubbell *et al.* 1999, presence of antagonists, Wirth *et al.* 2008). The excessive recruitment of *C. sciadophylla* in a single 1-ha plot and the unexpected collapse of *B. grossularioides* on Manaus forest edges illustrate the high degree of spatial heterogeneity in the distribution of short-lived pioneers along forest edges.

The ontogenetic-related response exhibited by some pioneer species is apparently shared with other tropical tree species, although responses may involve more than one ontogenetic stage and opposite directions. For example, forest fragmentation in the Manaus site reduced the density of seedlings and juveniles (5–400 cm tall) of the tree palm *Oenocarpus bacaba*, possibly due to failure in reproduction or increase in seed/seedling predation. However, *O. bacaba* recruitment into size class ≥ 10 cm was significantly greater in forest edges than interiors, indicating that subadults established before forest isolation were favored in forest fragments (Brum *et al.* 2008). It is likely that *O. bacaba* may be extirpated from the forest fragments in the long-term, but not owing to the suppression of adult recruitment. We can now suggest the inclusion of lifespan to the list of life-history traits that confer tree species sensitiveness to human disturbances (Tabarelli *et al.* 2004, Lopes *et al.* 2009, see also Ewers & Didham 2006).

A persistent decline of long-lived pioneer populations in edge-affected habitats may trigger a cascade of effects on forest dynamics in human-modified landscapes, *e.g.,* a 30 percent collapse on the aboveground biomass on forest edges (Paula *et al.* 2011). Large trees, such as the long-lived pioneers considered here: (1) account for 37 percent of aboveground plant biomass in Central Amazonia (Nascimento & Laurance 2002); (2) house many endemic bromelia species in the Brazilian Atlantic forest (Siqueira-Filho & Tabarelli 2006); and (3) provide sites for harpy eagle nidification in Mesoamerica (Ridgely & Gwynne 1993) and food resources for a great variety of vertebrates and invertebrates throughout the tropics (Gribel *et al.* 1999*,* Peres 2000, Arroyo-Rodríguez *et al.* 2007). Moreover, they are among the most commercialized goods in the international market of wood products (FAO [Food & Agriculture Organization of The United Nations] 2009), thus their decline along forest edges may significantly reduce the economic opportunities offered by forest habitats in human-modified landscapes.

In synthesis, by assessing the demographic structure of short- and long-lived pioneer tree species, we were able to document demographic responses of pioneer trees to forest edges and explore their potential impacts on the successional trajectory of edge-affected habitats. Nevertheless, a long-term monitoring of long-lived pioneer populations, particularly subadult/adult individuals, is required to offer conclusive evidence about the persistence of this key ecological group in human-modified landscapes. Also, a phylogenetically controlled approach considering a greater number of pioneer species is needed to accurately examine the role of lifespan in species persistence across altered landscapes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Study area.

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