

RESEARCH ARTICLE

# Influence of Post-Clearing Treatment on the Recovery of Herbaceous Plant Communities in Amazonian Secondary Forests

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## Abstract

Secondary forests are an increasingly common feature in tropical landscapes worldwide and understanding their regeneration is necessary to design effective restoration strategies. It has previously been shown that the woody species community in secondary forests can follow different successional pathways according to the nature of past human activities in the area, yet little is known about patterns of herbaceous species diversity in secondary forests with different histories of land use. We compared the diversity and abundance of herbaceous plant communities in two types of Central Amazonian secondary forests—those regenerating on pastures created by felling and burning trees and those where trees were felled only. We also tested if plant density and species richness in secondary forests are related to proximity to primary forest. In comparison with primary forest sites, forests regenerating on

non-burned habitats had lower herbaceous plant density and species richness than those on burned ones. However, species composition and abundance in non-burned stands were more similar to those of primary forest, whereas several secondary forest specialist species were found in burned stands. In both non-burned and burned forests, distance from the forest edge was not related to herbaceous density and species richness. Overall, our results suggest that the natural regeneration of herbaceous species in secondary tropical forests is dependent on a site's post-clearing treatment. We recommend evaluating the land history of a site prior to developing and implementing a restoration strategy, as this will influence the biological template on which restoration efforts are overlaid.

**Key words:** Central Amazonia, edge effect, fire, land-use history, regeneration, species diversity.

## Introduction

Secondary forests are a common feature in tropical landscapes (FAO 2007). In the Brazilian Amazon it is estimated that approximately 30% of the area that has been deforested is currently regenerating (Houghton et al. 2000). These secondary forests are an increasingly important component of conservation and restoration strategies (Chazdon et al. 2009)—in addition to acting as reservoirs of biodiversity and carbon, regenerating forests can facilitate inter-patch movement in fragmented landscapes and reduce edge effects (Brown &

Lugo 1990; Stouffer & Bierregaard 1995; Mesquita et al. 1999). Given the prevalence and importance of secondary forests, and the role they play in forest restoration programs, understanding the mechanisms that influence their regeneration has become an important area of research in tropical ecology.

In addition to factors such as soil quality and seed dispersal (Holl 1999), the regeneration of plant communities in tropical secondary forests can be influenced by the type and intensity of land-use (Uhl et al. 1988; Mesquita et al. 2001). For instance, Mesquita et al. (2001) have shown that secondary forests in Central Amazonia follow one of two regeneration trajectories based on how they were originally cleared. In areas where trees were felled and burned, secondary vegetation is dominated by pioneer tree species from the genus *Vismia* (Clusiaceae), resulting in secondary forest stands with low and open canopies, high understory light levels, and elevated air and soil temperatures. In contrast, regeneration in sites where fire was not used as part of the clearing process are dominated by pioneer tree species from the genus *Cecropia* (Cecropiaceae), whose taller canopies limit light penetration and result in a cooler, more humid understory. These floristic and structural differences have important consequences for the composition of woody plant communities—species richness

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is higher in unburned sites than in the burned ones, and there is little overlap in species composition between the two secondary forest types.

Whereas the succession of woody plant and palm communities in these and other secondary forests has been well described (Guariguata et al. 1997; Mesquita et al. 2001; Capers et al. 2005; Chazdon et al. 2007), our understanding of how other functional groups respond to forest regeneration remain limited (but see Costa & Magnusson 2002; Benítez-Malvido & Martínez-Ramos 2003). Herbaceous plants are a diverse, abundant, and ecologically important group of species in tropical rain forests (Gentry & Dodson 1987; Gentry & Emmons 1987; Poulsen 1996). In addition to being important resources for diverse communities of frugivores (Horvitz & Le Corff 1993), herbivores (Horvitz & Schemske 2002), and nectar-feeders (Stiles 1975; Kay & Schemske 2003), they are also economically important ornamentals (Berry & Kress 1991) and are used by traditional communities for handicrafts (Nakazono et al. 2004). Many aspects of their biology also suggest that their responses to forest clearing and fire will be different from those described for woody plants. For example, herbaceous plants are relatively small and, therefore, have shallower root systems than woody species (Canadell et al. 1996). Apart from the direct impact of fire, the subsequent changes in forest structure (Mesquita et al. 2001) could serve as an ecological filter permitting the regeneration of certain herbaceous species while impeding the establishment of others (Clark et al. 1993; Hooper et al. 2004).

Understanding patterns of regeneration can provide important insights into how to best approach the restoration of tropical ecosystems (Walker et al. 2007). To date, most restoration works on tropical sites have focused on trees (but see Leopold & Salazar 2008), in part because they are the key structural feature of forests. This focus on trees and the subsequent lack of data on the succession of other functional groups means that restoration efforts focusing on other life forms are rare. If the regeneration patterns of herbaceous species are distinct from those of woody plants, alternative forms of restoration will be needed to ensure a full complement of species is found in regenerating stands. We compared the diversity and abundance of terrestrial herbaceous plant communities in Central Amazonian secondary forests undergoing two distinct regeneration trajectories (Mesquita et al. 2001) with those in nearby primary forest. Our study addressed the following questions: (1) Do non-burned stands dominated by *Cecropia* spp. have more similar plant density, species richness, and species composition to primary forest than do locations that were burned and are now dominated by *Vismia* spp.? We predict that because fires can kill both established plants and seeds in seed banks, as well as affect regenerating forests' structure and understory environmental conditions, herbaceous plant communities in non-burned stands and primary forest will be more similar to each other than primary forest and burned stands; (2) In secondary forest stands, what is the relationship between proximity to primary forest and plant density or species richness? We predict that, given the potential for dispersal from primary forest, there is a positive relationship between proximity to

primary forest, population density, and species richness that is independent of the regeneration trajectory a secondary forest is undergoing.

## Methods

### Study Site and Sampling Design

This study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), located approximately 80 km north of Manaus, Brazil (2°30'S, 60°W). The diversity of trees in these *terra firme* forests is exceptionally high (de Oliveira & Mori 1999) and the understory is dominated by stemless palms (Scariot 1999). The soils in the region are primarily nutrient-poor oxisols with a high clay content and poor water-retaining capacity (Fearnside & Leal Filho 2002). Annual rainfall varies between 1900 and 2300 mm (BDFFP records) and the mean annual temperature is 26°C. The dry season extends from June to October.

BDFFP's secondary forests were created after the isolation of forest fragments in the early 1980s. The vegetation around the fragments was cleared and, in some cases, also burned. After the clearing, all areas were used as pasture for several years (reviewed in Bierregaard et al. 2002). Because there are two different kinds of secondary forests in the BDFFP landscape—those cleared only by felling trees (Fig. 1a) and those cleared by felling and burning (Fig. 1b)—the BDFFP is an ideal location in which to study the effects of alternative methods of forest clearing on the regeneration of plant communities.

We sampled the abundance and diversity of understory herbs in six of the BDFFP's secondary forests: three stands that were not burned (hereafter NB 1–3) and three stands that were burned after trees were felled (hereafter B 4–6). These stands were originally cleared between 1980 and 1984, and all of them are adjacent to a large, continuous expanse of primary forest. At the time we conducted this study (2003), the burned sites were between 19 (B6) and 23 (B4 and B5) years old. All of them were burned for the first time immediately after they were cleared, and for the last time between 1985 and 1988. One burned site (B6) was burned three times, whereas two (B4 and B5) were burned twice (Moreira 2003; BDFFP Records). All non-burned sites were 20 years old. In each of the six secondary forest stands, as well as in a primary forest stand adjacent to each secondary forest (hereafter PF 1-6; Fig. 2), we established a 250 × 100 m plot within which we randomly placed 25 subplots of 4 × 2 m. In secondary forests the plot was located 50 m from the secondary forest/primary forest border; in primary forest the plot was located 250 m from the edge to minimize edge-related effects on plant community composition and abundance (reviewed in Laurance et al. 2002).

We defined herbaceous plants as those without a woody stem (cf Raven et al. 2005). Under this definition, the groups Pteridophytae, Gymnospermae, Monocotyledoneae, and Dicotyledoneae all include some herbaceous species. However, we excluded lianas and species that do not spend their

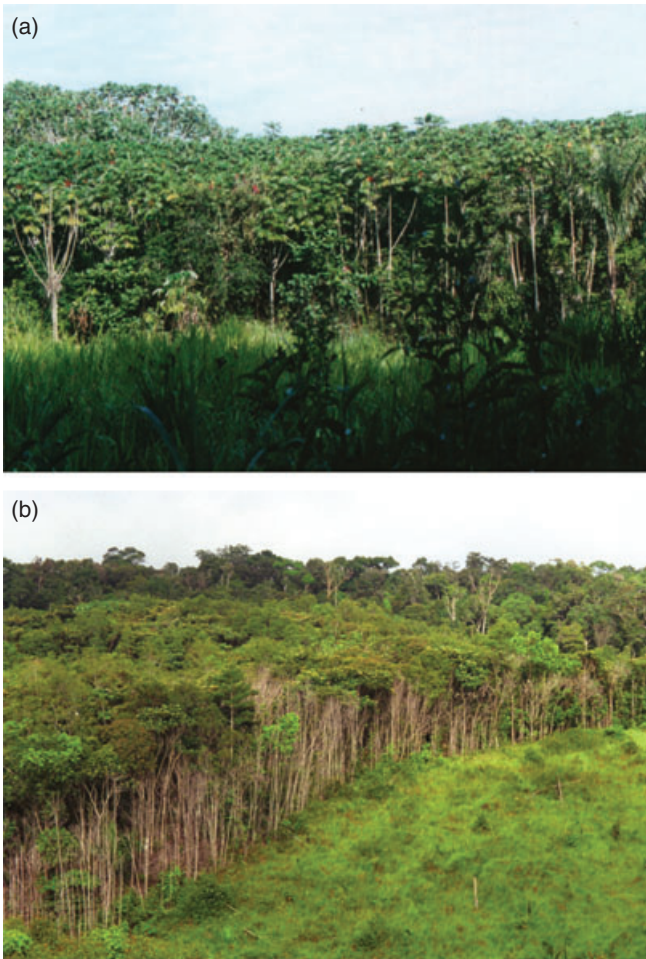


Figure 1. Secondary forest dominated by *Cecropia* spp. in a site where trees were only felled (a) and dominated by *Vismia* spp. in a site where trees were felled and burned (b), in BDFFP, Central Amazonia.

entire life cycle rooted in the forest floor (e.g. epiphytes, hemiepiphytes). Due to the difficulty in identifying very small individuals, we sampled only individuals  $\geq 5$  cm in height (following Costa & Magnusson 2002). From July to October 2003 we counted and identified all herbaceous individuals rooted in 25 subplots in each plot. Plants with vegetative reproduction were considered different individuals if their shoots were not visibly linked. Individuals we were not able to identify in the field were collected for later identification at the herbarium of the National Institute for Amazonia Research (INPA).

#### Statistical Analyses

We compared the density of plants in each secondary forest site with that in the adjacent primary forest using two randomized block analyses of variance (ANOVA; Zar 1996): one for burned stands paired with adjacent primary forest and other for non-burned stands paired with adjacent primary forest

sites. The different locations (1–6) were blocks and the forest types (non-burned stand/burned stand, primary forest) were the treatments. Data were log-transformed to meet the assumptions of the ANOVA. Species richness was compared using two methods. First, we used rarefaction curves of the number of species based on individual number (Gotelli & Colwell 2001). For each site we used 1,000 randomizations of individual sequence and compared the number of species for the same number of individuals. Second, we estimated the number of species in each site using the nonparametric estimator Chao 2, which is based on the presence and absence of species in the samples (Colwell & Coddington 1994). Analyses were conducted using the EstimateS software package (Colwell 1997).

The similarity of species composition between the sites was evaluated using the Jaccard similarity index, based on species incidence (Magurran 2004), and the abundance-based Chao–Jaccard index (Chao et al. 2005), which includes the effect of unseen species. To better visualize the similarity between the sites we used a multidimensional scale analysis (MDS) applied over the above-cited association matrices, using 50 runs for each analysis. We also built, for each site, species rank abundance plots (Magurran 2004) where every species found in a site was ranked from the most to the less abundant, to compare the relative abundance of species in the different forest types. These analyses were performed using EstimateS and Systat 8.0 (SSI 2001).

To test the prediction that herbaceous plant density increases with increasing proximity to primary forest, we used an analysis of covariance (ANCOVA; Zar 1996), with the log-transformed density of plants in each subplot as the dependent variable, the different locations (1–6) as the factor, and the distance of the subplot from the primary forest edge as the covariate. To test the prediction that the number of species in secondary forest increases with increasing proximity to primary forest, we used a two-way ANOVA; we compared the number of species in groups of subplots located at increasing distances from the primary forest edge (50–80, 85–115, and 120–150 m), considering the different locations as one of the factors. We conducted both analyses separately for burned and non-burned secondary forests.

#### Results

We identified 3,369 individuals from 52 species in 23 families. Seven species were Pteridophytes, one was a Gymnosperm, and 44 were Angiosperms, of which eight were dicots and 36 were monocots. The family Marantaceae was the most commonly observed (11 species), followed by Cyperaceae and Poaceae (both s7 species). Of the 52 species recorded, 13 were found in all three forest types, whereas 15 species occurred exclusively in the primary forest, three species were found solely in non-burned stands, and seven were only recorded in burned stands. The most widespread species were *Heliconia acuminata* (Heliconiaceae), which was found in all sites, and *Calathea altissima* (Marantaceae), which was found in all sites but one.

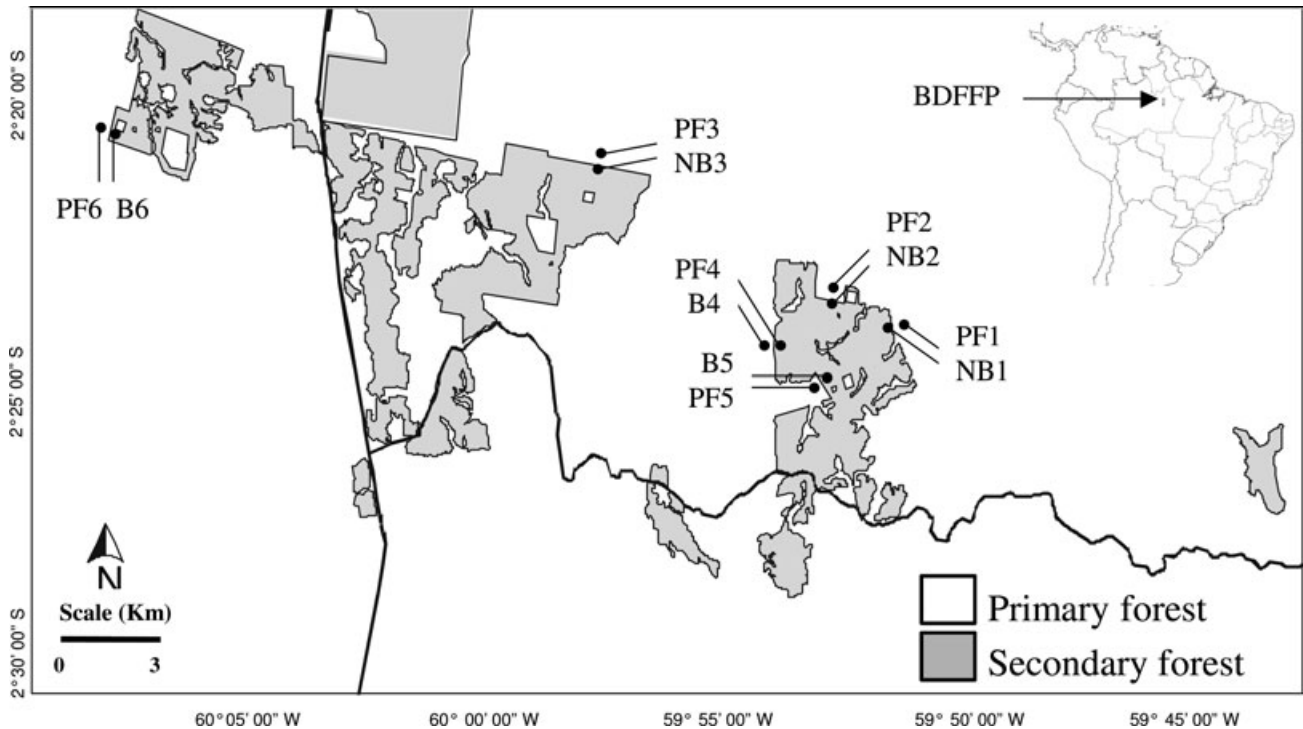


Figure 2. Map of the BDFFP sites, Central Amazonia, in which our surveys were conducted. The dots indicate the non-burned stands (NB), burned stands (B), and primary forests sites (PF) sampled.

### Density of Individuals

In contrast to our prediction, mean plant density was 2.7–18.9 fold lower in non-burned stands than in adjacent primary forest sites, a highly significant difference ( $f = 90.9$ ,  $ms = 82.52$ ,  $df = 1$ ,  $p < 0.001$ ). However, density in burned stands and adjacent primary forests was not significantly different (range: 3.5 fold lower to 3.1 fold higher;  $f = 0.1$ ,  $ms = 0.04$ ,  $df = 1$ ,  $p = 0.83$ ). Overall, the mean density of herbs per subplot was lowest in non-burned stands ( $3.4 \pm 5.3$  SD; range 0–37), intermediate in burned stands ( $8.3 \pm 22.0$  SD; range 0–186), and highest in the primary forest ( $16.6 \pm 35.3$  SD; range 0–276).

### Species Richness

Pooling data from all stands within a forest type resulted in 22 species in non-burned stands, 28 in burned stands, and 42 in primary forest. Because no rarefaction curves reached an asymptote (Fig. 3), a greater sampling effort is needed to determine the true species richness in each habitat type. Based on the nonparametric estimator Chao 2, estimated species richness ranged from  $15.3 \pm 2.3$  (mean  $\pm$  SD) to  $17.2 \pm 5.3$  in non-burned stands, from  $14.5 \pm 0.0$  to  $30.6 \pm 12.5$  in burned stands, and from  $12.2 \pm 5.3$  to  $42.7 \pm 28.6$  in primary forest sites.

### Patterns of Species Abundance and Composition

Both the Jaccard and the Chao–Jaccard indices indicated the highest similarity values between non-burned sites and primary

forest sites or primary forest sites with one another. The MDS for both Jaccard and Chao–Jaccard indices separated burned sites from non-burned and primary-forest sites (Fig. 4). The reduction of the data in two dimensions by the MDS explained 91 and 93% of the total variation in the data for Jaccard and Chao–Jaccard indices, respectively.

The rank abundance plots constructed for each site all had similar patterns: a few common species and many rare ones (Fig. 5). Some species are abundant in all forest types (e.g. *H. acuminata*, *C. altissima*), whereas others are abundant but occur almost exclusively in primary forests (e.g. *Lindsaea lancea* (Dennstaedtiaceae)). In general, species that are at high density in primary forest are more commonly found in non-burned than burned stands (e.g. *Selaginella* spp. (Selaginellaceae)). However, the majority of species that were rare in primary forest was not found in either secondary forest type (e.g. *Metaxia rostrata* (Metaxiaceae), *Olyra ramosissima* (Poaceae)). Notably, most species with high abundance in burned stands (e.g. *Rolandra fruticosa* (Asteraceae), *Actinostachys subtrijuga* (Schizaeaceae), *Scleria secans* (Cyperaceae), *Geophila cordifolia* (Rubiaceae)) were rare or absent in the other forest types.

### Proximity to Primary Forest Versus Plant Density and Species Richness

Distance from the forest edge did not affect either plant density (non-burned sites:  $f = 0.8$ ,  $ms = 0.516$ ,  $df = 1$ ,  $r^2 = 0.021$ ,  $p = 0.382$ ; burned sites:  $f = 3.0$ ,  $ms = 2.461$ ,  $df = 1$ ,  $r^2 =$

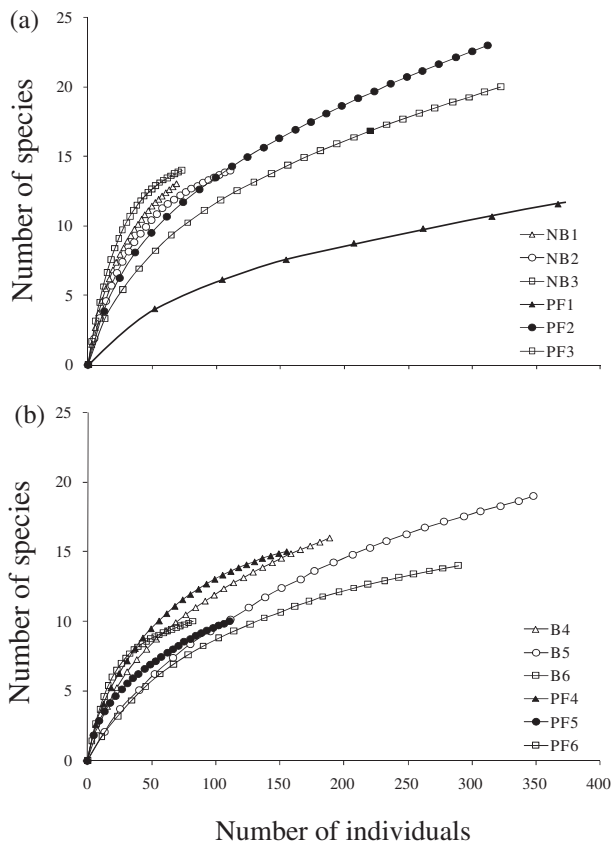


Figure 3. Rarefaction curves of the cumulative number of terrestrial herbaceous species by the number of sampled individuals for non-burned stands and adjacent primary forest sites (a), and for burned stands and adjacent primary forest sites (b), in BDFFP, Central Amazonia.

0.139,  $p = 0.088$ ) or species richness (non-burned sites:  $f = 0.2$ ,  $ms = 0.778$ ,  $df = 2$ ,  $p = 0.850$ ; burned sites:  $f = 1.8$ ,  $ms = 8.111$ ,  $df = 2$ ,  $p = 0.273$ ) in any of the secondary forests studied.

**Discussion**

Our results suggest that the means by which tropical forest is cleared strongly influences the regeneration patterns of herbaceous plant communities. Contrary to our predictions, fire appears to have less severe impacts on density and richness than creating pastures by only felling trees. However, the unexpected high density and species richness observed in burned stands are attributable primarily to an influx of disturbed habitat specialist species in these sites (22.8–60.1% of the individuals, 7 species vs. 1.4–15.1% of the individuals, 3 species in non-burned sites). In addition, herbaceous community composition at non-burned stands is more similar to that of the adjacent primary forest, suggesting there are important ecological consequences of fire for the regeneration of these plant communities.

The germination of seeds from seed banks probably played a fundamental role in the regeneration of herbaceous forest

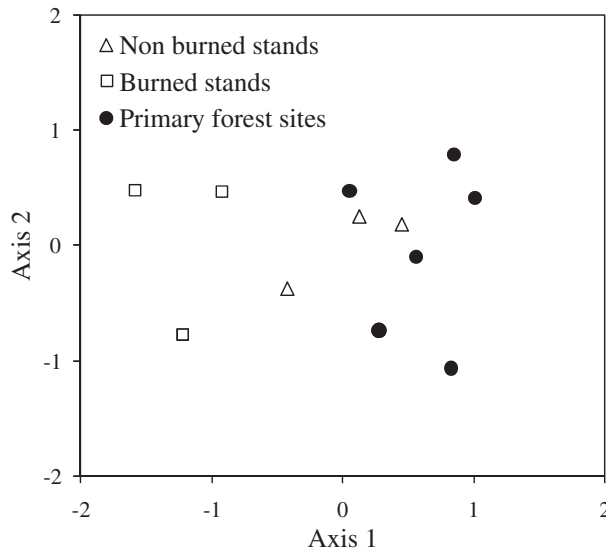


Figure 4. Multidimensional scaling analysis of herbaceous species estimated abundance in non-burned stands, burned stands, and adjacent primary forest sites of BDFFP, Central Amazonia.

species in non-burned stands. In contrast, because fire may have dramatically reduced the seed bank in burned stands (Monaco et al. 2003), it is likely that in these sites resprouting and vegetative propagation following clearing were probably of key importance (see also Hooper et al. 2004). Indeed, the most common forest species in our burned sites were those with belowground storage structures that can resprout (e.g. *Heliconia acuminata*, *Calathea altissima*).

It is worth noting, however, that fire per se may not have been the main driver of succession. Instead, the contrasting forest structure and environmental conditions created by the dominant pioneer species in each forest type (e.g. *Vismia* spp. or *Cecropia* spp.) may have had a major effect on the herbaceous trajectory of succession. For instance, previous studies showed that there are marked differences in canopy openness between burned stands and non-burned stands (Ribeiro 2005). In non-burned stands, the dense canopy of *Cecropia* trees, with their large leaves, creates a more shaded and cool environment that may be more suitable for understory species typically found in the primary forest. The most abundant species in most primary forest and non-burned sites, *Selaginella* spp., was never observed in burned stands. The same is true for *Trichomanes pinnatum* (Hymenophyllaceae), for which we recorded only a single individual in one burned stand. Because *Selaginella* spp. and *T. pinnatum* are pteridophytes, they may be highly sensitive to desiccation. In burned stands the less dense canopy probably results in elevated temperature and reduced humidity at the forest surface. Many herbaceous species may not tolerate such conditions (reviewed in Bazzaz & Pickett 1980), which could act as an ecological filter permitting the regeneration of only certain species, such as the secondary forest specialists we found. We believe that the ability of *Vismia* spp. to resprout has perpetuated environmental conditions found in

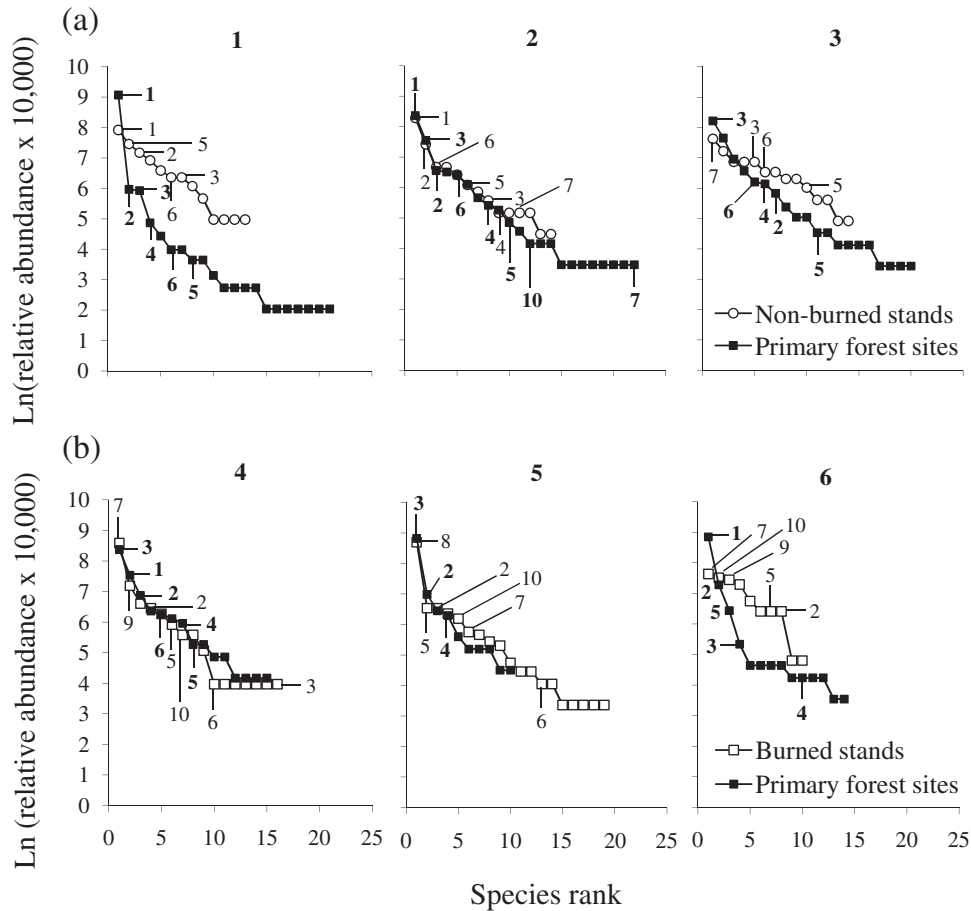


Figure 5. Rank abundance plots of terrestrial herbaceous species in (a) non-burned stands and adjacent primary forest sites and in (b) burned stands and adjacent primary forest sites in BDFFP, Central Amazonia. The five most abundant species in each type of habitat are represented in the plots: 1 = *Selaginella* spp., 2 = *Heliconia acuminata*, 3 = *Trichomanes pinnatum*, 4 = *Lindsaea lancea*, 5 = *Calathea altissima*, 6 = *Adiantum* spp., 7 = *Scleria secans*, 8 = *Rolandra fruticosa*, 9 = *Actinostachys subtrijuga*, 10 = *Geophila cordifolia*. The highlighted numbers represent the position of the species in the primary forest sites, and the numbers in normal style the species in the secondary forests. The relative abundances are in logarithmic scale and species are positioned from the most to least abundant.

burned sites for many years following the initial disturbance, limiting regeneration of primary forest understory species.

The patterns we observed may be also driven by differences in litter depth between secondary forest types. Due to the high volume of *Cecropia* leaves, non-burned stands have deeper litter layers than burned sites (Ribeiro 2005). While litter can have positive effects on the germination of some species by providing favorable microenvironmental conditions and diminishing the chance of predation (Cintra 1997; Ganade & Brown 2002), deep litter can also bury the typically smaller seeds of herbaceous plants (Moles et al. 2005) and expose them to fungal pathogens (Molofsky & Augspurger 1992; Bruna & Ribeiro 2005). The differences in forest structure and woody species composition between burned and non-burned sites may also have influenced their use by seed dispersers, thereby influencing the levels of similarity between recovering areas. Previous work conducted at the BDFFP has demonstrated that more species of frugivorous birds occur in non-burned than in burned stands in the first years of succession (Bierregaard

& Stouffer 1997); it is therefore likely that the diversity and abundance of forest seeds dispersed into burned stands could be substantially reduced despite their proximity to primary forest.

It is noteworthy that herbaceous species that were rare in primary forest were usually missing from both non-burned and burned stands. Although this could be because these species were absent prior to forest clearing, it could also be a result of post-clearing extinction of small populations. Such a loss of rare species was observed for herb, liana, palm, and tree seedlings recruiting in forest fragments in BDFFP (Benítez-Malvido & Martínez-Ramos 2003). While rare species can disappear from disturbed landscapes because they have more specific environmental requirements (Meier et al. 1995), they are also more susceptible to the effects of demographic and environmental stochasticity. Even if environmental conditions are suitable for plant establishment and growth, the limited number of propagules dispersing from nearby forests may accentuate the delay in the recovery of these species.

An interesting result from our study is the conspicuous lack of edge effects on plant abundance and diversity in secondary forests. This result contrasts with previous studies which found that seedling and woody plant diversity in recovering areas are strongly influenced by distance from the forest edge (Aide & Cavelier 1994; Mesquita et al. 2001; Hooper et al. 2004). However, previous studies have also shown that most seeds dispersed from forest to abandoned pastures travel no more than 10 m (Aide & Cavelier 1994; Holl 1999; Cubiña & Aide 2001), and edge effects on woody plant richness and density are most evident within 50 m of the forest edge (Mesquita et al. 2001). Although we may have failed to detect an edge effect only because we sampled beyond the extent at which the effects manifest themselves, our results nevertheless suggest that for herbaceous plants the distance from the forest does not affect recovery.

Our results also yielded a curious pattern—burned sites are more heterogeneous than non-burned sites (based on the standard deviation of density and richness, rarefaction curves, and MDS analysis). The most plausible explanation is that the burned sites we evaluated have a more variable history than non-burned ones. While all non-burned sites were of the same age, one of the burned stands was four years younger than the others. Furthermore, the burn history was slightly different between stands. The first burn in all sites occurred immediately after clearing, but the last burn occurred 1–4 years after clearing. Moreover, two stands were burned twice and one stand was burned three times. Finally, some of the secondary forest species we found in burned sites occurred in high-density aggregations (e.g. *Rolandra fruticosa*, *Scleria secans*), resulting in a high variability of plant density in these sites.

Our results demonstrate that after 20 years of succession, natural regeneration was not enough for the herbaceous community in either burned or non-burned sites to fully recover. Furthermore, the use of fire to create pastures delayed the succession of herbaceous plant communities in secondary forests, corroborating the results from previous work on woody taxa conducted in the same study site (Mesquita et al. 2001). Although sites that are near large expanses of primary forest appear likely to naturally regenerate to states that resemble the original forest (Finegan 1996), our results suggest this is not the case for herbaceous species, because we did not detect an edge effect and several species are missing from the community, especially in burned sites. As such, those sites may require more active restoration management to regain the full complement of species and thus reestablish biodiversity and ecological processes (Lamb et al. 1997; Chazdon 2008).

We suggest that the first step toward the recovery of the herbaceous community in regenerating Amazonian sites is to protect them from fire, which can kill both established individuals and deplete the seed bank. Because previous work has shown that small seeds often suffer high rates of predation in secondary forests (Garcia-Orth & Martinez-Ramos 2008) and that germination rates of seeds in regenerating forests can be low but that seedling survivorship can be reasonably high (Bruna and Ribeiro 2005), we also suggest the transplanting of established seedlings, rather than seed sowing, to establish

species that do not colonize naturally (Mottl et al. 2006; Shono et al. 2006). The efficacy of this labor-intensive strategy, however, may require environmental conditions in burned site's understory, such as high light levels and leaf-litter depth (Ribeiro 2005), be improved to promote plant survivorship.

Besides evaluating the effects of fire on the recovery of herbaceous species in secondary forests, our study provided information about structure and composition of herbaceous communities in primary forests of Central Amazonia. Such information can serve as a template to the design of the restoration strategies as well as to evaluate restoration success in tropical sites near ours (Lane & Texler 2009). In addition, despite the fact that our secondary forest sites contain only a portion of the total species pool observed in primary forests, they nonetheless harbor a great diversity of herbaceous plants. They therefore serve as sources of propagules for the recovery of newly created pastures during restoration, and may play a fundamental role in maintaining biodiversity at the landscape scale (Brown & Lugo 1990; Chazdon et al. 2009).

#### Implications for Practice

- Regenerating sites should be protected from fires, which can kill both established individuals and seeds in the seed bank, impede the accumulation of species with narrow tolerances to environmental perturbations, and result in the invasion of generalist species.
- Restoration strategies should consider a site's fire history. Sites that have been burned are likely to lack many forest herbaceous species and have species abundance altered, and therefore are more likely to need reintroduction of those species than non-burned sites.

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