

Amazon Rain Forest Succession: Stochasticity or Land-Use Legacy?

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*Land-use practices can dramatically shift the trajectories of rain forest recovery. In a 25-year study, Amazon rain forest regenerated following deforestation as long as seed availability and seedling recruitment were not interrupted. In contrast, rain forest converted to cattle pastures via cutting and burning prior to abandonment diverted succession, leading to highly simplified stands dominated by a single genus. Annual fires eliminated seedlings, saplings, coppice, and seeds in the soil, except for several *Vismia* species. Once established, *Vismia* regenerated by continual resprouting and resisted the establishment of other rain forest species, especially the normal suite of pioneers. Through time, succession both in abandoned clearcuts and pastures increased in stem density and biomass; however, species accumulation and ecosystem services were limited in pastures when compared with those in abandoned clearcuts. Therefore, prescribed burning to maintain pastureland leaves a legacy that is not readily extinguished, whereas abandoning clearcuts engenders an accelerated rain forest regeneration.*

Keywords: secondary succession, forest regeneration, alternative pathways, land-use history, stochastic processes

One paradigm of plant succession is that the abiotic environment determines the pathway of vegetation changes, leading ultimately to a relatively stable species assemblage (Clements 1916). Underlying the predictability of secondary succession is the availability of the component species—that is, species' replacements are not limited by the absence of seeds, seedlings, or other regenerative propagules of the various successional stages (Egler 1954).

More recent studies have shown that biotic factors can be as important as the abiotic environment and act as filters for the species assemblages, with a resulting diversity of community outcomes (Webb et al. 2002, Letcher et al. 2012). The phylogenetic structure of tropical successional communities can help define the relative importance of biotic and abiotic factors. Letcher and colleagues (2012), investigating three very distinct Neotropical sites, including our study plots, showed an increasing role of biotic processes in shaping the plant community as succession proceeds. Therefore, for tropical rain forests, the predictability of succession has been challenged following empirical demonstrations of exceptional variability in structural attributes and species composition of secondary forests of the same age (Chazdon et al. 2007). Such variability is so high that studies of chronosequences—nearby stands of different ages since abandonment—show little resemblance to a temporal sequence of any individual stand. Despite sharing identical soils and climate, contiguous secondary forests—presumed to share land-use histories—exhibit different species

assemblages (Guariguata and Ostertag 2001, Chazdon et al. 2007, Walker et al. 2010) and can develop different community attributes (e.g., basal area, plant height, or floristic diversity) at different rates, resulting in low predictability of chronosequence outcomes (Mora et al. 2015). In the case of the Amazon, within the 20- to 40-year time frame studied, there is little tendency for convergence in community composition as successional trajectories unfold through time (Longworth et al. 2014, Williamson et al. 2014).

The extreme species richness and complexity of tropical forests have been offered as a possible cause for the uncertainty in rain forest successions (Walker et al. 2010). The variability in species composition could be attributed to the vagaries of seed dispersal and survival that could limit the timely recruitment of different tree species along successional pathways (Suding et al. 2004, Young et al. 2005). Among tropical ecologists, stochasticity induced by dispersal limitation and high diversity has become a provocative null hypothesis for old-growth forest assembly (Hubbell 2001). If climaxes are haphazard assemblages from rich species' pools, then successional sequences could surely share the same uncertainty. Although initial species composition is an old theme in plant succession (Egler 1954), predictable species' turnover in temperate forest succession has lessened its importance. However, the potential number of initial assemblages in tropical rain forests invites renewed interest in the possible stochasticity of secondary succession.

Further complicating the interpretation of tropical succession is prior land-use history. In all ecosystems, anthropogenic practices are expected to affect successional trajectories, sometimes through changes in the physical and chemical properties of an ecosystem and sometimes through biotic alterations. In tropical rain forests, prior land use is extremely variable in space and time and known only anecdotally, thereby precluding the causal association of successional trajectories. Although the importance of land-use history in shaping species composition is acknowledged (Mesquita et al. 2001, Thompson et al. 2002, Chazdon et al. 2007), it has been overlooked in many cases because assessing past land-use practices is not always possible.

In the central Amazon, regrowth follows two main land use practices: pasturelands and shifting cultivation, which are both managed by slash and burn. Following deforestation, the cleared and burned land may be planted in any number of annual and perennial crops—such as manioc, pineapple, bananas, açai palm, nut trees—or seeded with exotic grasses for conversion to pasture. In the Amazon Basin, pastoral uses are accompanied by annual or occasional burning to renew grasses, deter woody recruitment, and slow down plant succession. In shifting cultivation, fallows are burned after they have been cut in order to clear the land and fertilize the soil for the next cropping period. However, after various pastoral and agricultural trials, soil nutrients, already low from 250 million years of leaching, are exhausted, so lands may be abandoned completely. Thereafter, as plant colonization occurs, the land undergoes succession along a trajectory influenced by the legacy of land-use practices. However, land-use history is rarely recorded. Furthermore, land use is so variable that adjacent landholdings are unlikely to represent replicate treatments in fire regime, the number of prunings, the legacy effects of crop cultivation, and subsequent mineralization.

Does land-use history determine tropical successional trajectories?

To control variability in land-use history, we used a large-scale experiment to determine the effects caused by two of the most important land-use treatments in the Amazon Basin: In the clearcut treatment, all trees are cut and the usable timber extracted, leaving stumps and slash with no or one light burn before abandonment; in the pasture treatment, trees are similarly cut and timber extracted, but then stumps and slash would be burned and the land subsequently seeded with exotic grasses, grazed by cattle, and burned annually for 5–8 years before abandonment (figure 1). The clearcuts, de facto, represent the minimal perturbation from deforestation in that stumps and seedlings are left to sprout and the seed bank left to germinate, whereas the soil physical and chemical properties are largely unchanged. In contrast, the pasture treatments represent a “scorched-earth” anthropogenic disturbance in which trees and seeds from the original forest composition would be

suppressed by burning and by competition with exotics, whereas soil might be compacted and eroded because of cattle grazing. Changes in nutrients and soil microbes might also be expected in the pasture treatment.

We found a suitable research site at the Biological Dynamics of Forest Fragments Project (BDFFP). Initiated in the early 1980s, five large farms in the central Amazon were created north of Manaus, Brazil, by deforestation. The farms are spread over more than 1000 square kilometers. Some portions of the farms were abandoned immediately after deforestation whereas others were converted to pastures and then grazed and burned for several years prior to abandonment. Some are still kept in pasture with annual burnings. Because the farms were large (over 3000 hectares) and created nearly simultaneously, the two treatments—clearcuts versus pastures—were replicated dozens of times. In this study, we'll refer to the two treatments as (1) “clearcuts” or “*Cecropia* stands” and (2) “pastures” or “*Vismia* stands,” emphasizing the consistency of the dominant species associated with each land-use history. Individual farms had the two treatments in different portions of areas (e.g., Colosso and Dimona farms; figure 2), and for this reason, we refer to areas within treatments. Twenty-two replicated transects are the independent sample units. Clearcut areas were not burned, although in a few cases, a light burning occurred once. Abandoned pastures were burned anywhere from two to over nine times before we established our study transects. There were no plots of agriculture, agroforestry, or plantation forestry on the study sites (see Longworth et al. 2014 for a more complete description of individual transects' history and location).

A treatment such as clearing, burning, and conversion to pasture must be implemented over a large block of land in order to experimentally replicate human land use. Chronosequences have been shown to misrepresent true temporal change in individual blocks (Chazdon et al. 2007, Walker et al. 2010). Multiple study plots on a single treatment block are considered pseudoreplication (Hurlbert 1984); therefore, to achieve replication while controlling land-use histories, our 22 study transects were scattered across five farms (Porto Alegre, Dimona, ZF-7, Colosso, and Diva), spread across 50 kilometers (km) east–west at a latitude of 2 degrees south. The history of each study area within each farm was determined by land-use records and closely corroborated by review of Landsat images from 1980 to 1995, thanks to NASA's Large Scale Biosphere–Atmosphere Project in the Amazon (Moreira 2003). The areas are scattered throughout the secondary forest matrices surrounding primary forest fragments at the BDFFP, and the farms are embedded in a common landscape of primary forest (see article by Stouffer et al., this issue). Although both treatments were deforested together, the clearcuts, which were abandoned immediately, initiated succession first, and for this reason, they are several years older (5–31 years) than the abandoned pastures (2–25 years) as of 2014. The data set represents 15 successive years of annual censuses.

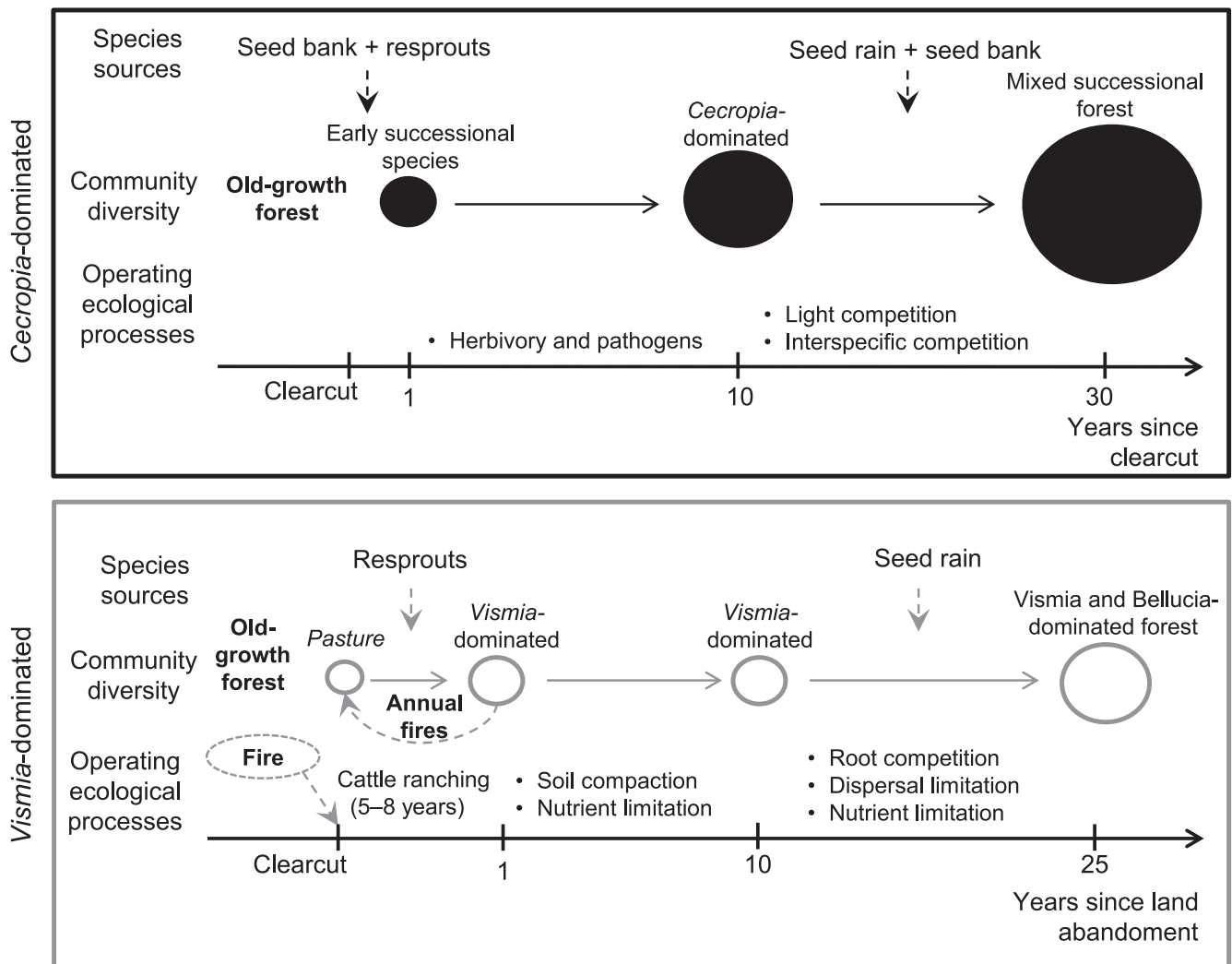


Figure 1. A conceptual diagram describing the main operating biotic and abiotic processes involved in structuring successional communities in the two successional trajectories described in this study for central Amazonia. Note that relevant ecological processes and biotic interactions change through time and between successional trajectories and differentially affect the plant communities described. As a result, community floristic diversity evolves at different rates and reaches different outcomes, given relatively similar time frames for the processes to operate.

Regeneration: Stems

Succession following the two land-use treatments has been dramatically and consistently different in several ways. In the clearcuts, stem density (more than or equal to 3 centimeters diameters at breast height; cm dbh) rose immediately with abandonment as surviving seedlings, stump sprouts, and emerged seedlings provided a ready source of regenerating plants. Within five years, density in the clearcuts reached a plateau, where it has remained unchanged for the subsequent two decades, resembling regeneration in large forest gaps (figure 3). In contrast, the abandoned pastures were largely devoid of woody recruitment except for three species of *Vismia*, the only genus capable of prolific resprouting after fires. Other genera originating as stump sprouts or as seedlings that emerged from the seed bank had been largely eradicated by the prescribed annual burns. With mainly

scattered clumps of *Vismia* resprouts, the density of young trees in the pastures started low but unfolded like a wave of stems in an even-aged stand. By the end of a decade, the density of stems reached an unsustainable level, self-thinning ensued, and the density declined to approximate the stem density in the abandoned clearcuts (figure 3).

Regeneration: Biodiversity

The old-growth rain forest in this part of the Amazon contains well over a thousand tree species, providing a hyperdiverse species pool for regenerating forests. The clearcut treatments, although dominated by the pioneer genus *Cecropia* (mainly *C. sciadophylla* and *C. purpurascens*) in the canopy, harbored many other species as seedlings and small saplings. In contrast, the abandoned pastures, dominated by *Vismia* spp, were initially very depauperate in species.

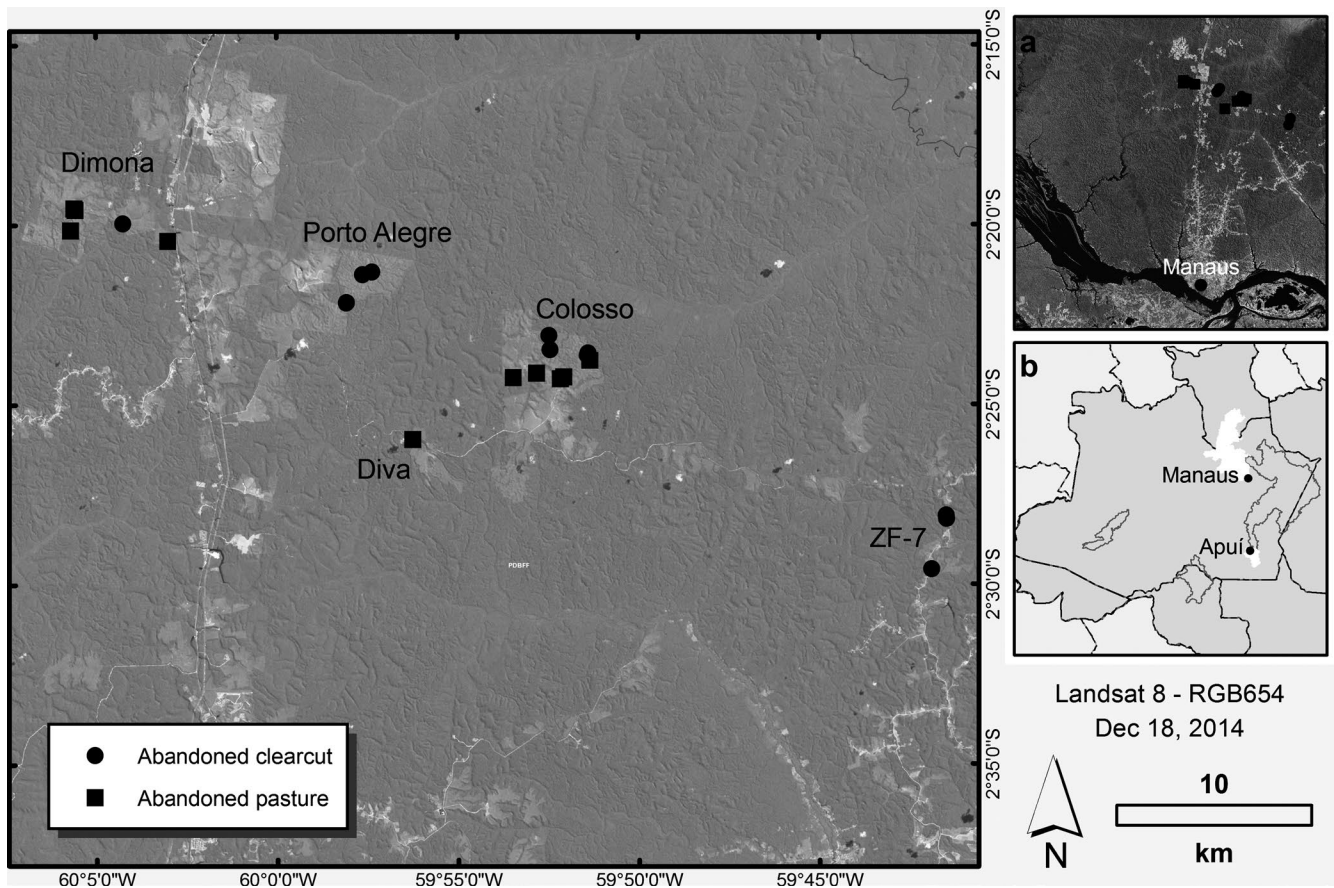


Figure 2. A map of the study sites, indicating farms (identified by their names) and transect locations for clearcut (black circles) and pasture treatments (black squares), with some areas overlapping. Native forests are represented in darker gray colors; the whitish and lighter gray colors represent pasturelands and secondary forests, respectively. The smaller maps at the upper right show (a) the Biological Dynamics of Forest Fragments Project transects in a broader scale in relation to Manaus and (b) the five watersheds across the state of Amazonas where data has been collected on secondary succession, highlighting the Apuí and Manaus watersheds (white polygons), whose floristic composition is compared here. Abbreviation: km, kilometers.

The initial difference is not surprising given the harshness of pasture conversion and competition with grasses, but to our surprise, the difference in species accumulation continued and increased through time. Species richness increased in the clearcuts at a pace about threefold faster than the increase in the abandoned pastures (figure 4). Even after two decades, the differences in the rate of addition of new species persisted, so the pastures increasingly fell behind the clearcuts in biodiversity. After two decades, a study plot of 200 trees contained over 80 species in the abandoned clearcuts but fewer than 40 in the abandoned pastures.

One consequence of the rapid species accumulation in the clearcuts was a divergence in species composition (figure 5). To test whether the transects were diverging significantly through time, we calculated the Euclidean distances among points representing the measurements taken in the first and the last monitoring periods of each transect monitored through time, in the ordination space of the nonmetric multidimensional scaling (NMDS; figure 5). We then tested

whether the distances among initial points and among final points were different between treatments and within treatments. The comparisons between treatments showed that the final points of the clearcuts were more distant among each other than the final points of the pasture transects ($t(31.56) = 6.63, p < .0001$; table 1); within treatments, the initial and final distances were also significantly different. The final points of clearcut successions were more distant to each other than the initial points ($t(54) = 2.3766, p = .01$; table 1). Contrasting, final points of pasture successions were closer to one another than initial points ($t(22.389) = -4.5251, p < .0001$; table 1).

As the clearcut transects became more diverse through time, they became more different from one another (table 1), because as dominance by pioneer species dissipated, a heterogeneous set of forest species established in the different transects. Such variation is expected, because these systems are moving through successional stages toward the highly diverse mature forests, which themselves exhibit low floristic

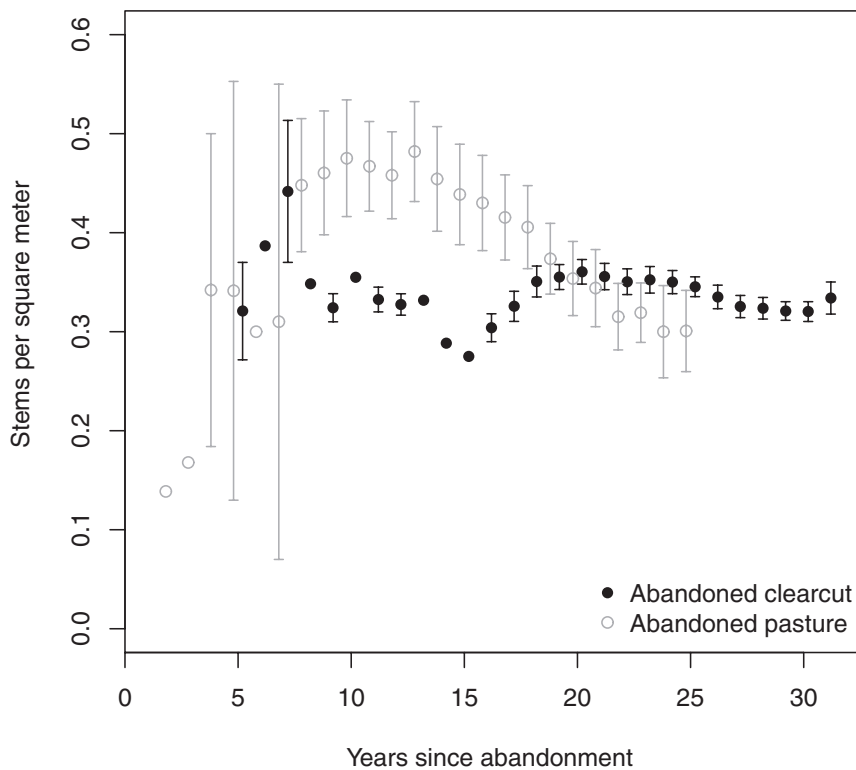


Figure 3. The mean density of stems (more than or equal to 3 centimeters diameter at breast height) as a function of transect age in abandoned clearcuts (black circles) and in abandoned pastures (gray circles). The error bars indicate the standard error.

similarities among adjacent stands (Oliveira and Nelson 2001, Steege et al. 2003). In contrast, dominance by *Vismia* in the abandoned pastures remained, sometimes shared with another genus, *Bellucia*. Consequently, after two decades, the pasture transects exhibited little divergence from one another in species composition (figure 5), remaining more similar among themselves than patches of the clearcut transects did (table 1), as well as more similar to each other through time (table 1).

Close inspection of figure 5 reveals that the first dimension (NMDS 1) separates the study transects by land-use history (i.e., pasture and clearcut). The second dimension (NMDS 2) seems to reflect the increasing change in species diversity over time, because pasture stands show a clustering of young stands toward the negative values of NMDS 2 and a slight increase toward more positive values with age. The clearcuts were notably divergent over time, because new species were added to the pool in this highly diverse community.

To test the hypothesis that species composition differs among land uses and that this divergence remains over time, we applied a distance-based redundancy analysis (Legendre and Anderson 1999). We included the land-use treatments (clearcut and pasture), successional age, and the interaction between treatment and age as predictors for species composition weighted by basal area. Transects were included

as covariables to account for the dependency between measurements of the same transect through time (Legendre and Anderson 1999). The first three axes of the distance-based redundancy analysis (RDA) explained half of the variation in species composition (51.8%; table 2). Of this total variation explained, 73% was explained by treatment (clearcut and pasture), 17% by successional age, and 10% by the interaction between treatments and age (table 2). The first axis explained 38% of the variation and was strongly correlated with treatment ($r = -.96$), the interaction between age and treatment ($r = -.84$), and, to a lower extent, successional age ($r = .41$). The second axis explained an additional 10% of the variation in species composition and was strongly correlated with successional age ($r = .59$) and the interaction between age and clearcut ($r = .58$) but less with the interaction between age and pasture treatment ($r = -.33$). The different directions of the correlation between the interaction terms and the axes indicate that age has a divergent effect on each treatment.

These results show that past land use greatly determines species composition, because land-use treatments explained half of the variation in species composition. Successional age had a relatively low contribution to determine species composition, which is related to the fact that the effect of successional age depends on land-use treatment. The effect of successional age was stronger in the clearcut ($r = .76$) than in the pasture treatment ($r = -.21$). The ordination of the plots and the direction of the correlations between age and the effect of age at each land-use type indicate successional age pointing to different directions at each land-use type (table 2). These results indicate that the two successional trajectories are consistently different and continue to diverge through time.

Causes of the two successional trajectories

Abandoned pastures potentially differ from clearcuts in two broad categories: soil conditions and initial floristic composition. In South America, the soil properties of cattle pastures are known to diverge from adjacent forest soils in deciduous forests and savannas (Abril and Bucher 1999, Pereira et al. 2001, Álvarez-Yépez et al. 2008). Nutrient losses in pastures derived from rain forests might be expected as well, given that soil exchange capacities in the central Amazon are exceptionally low. However, cation concentrations seem to be unrelated to land-use history throughout the Amazon (Uhl 1987, Buschbacher et al. 1988, Feldpausch et al. 2004, 2007). Specifically at our sites,

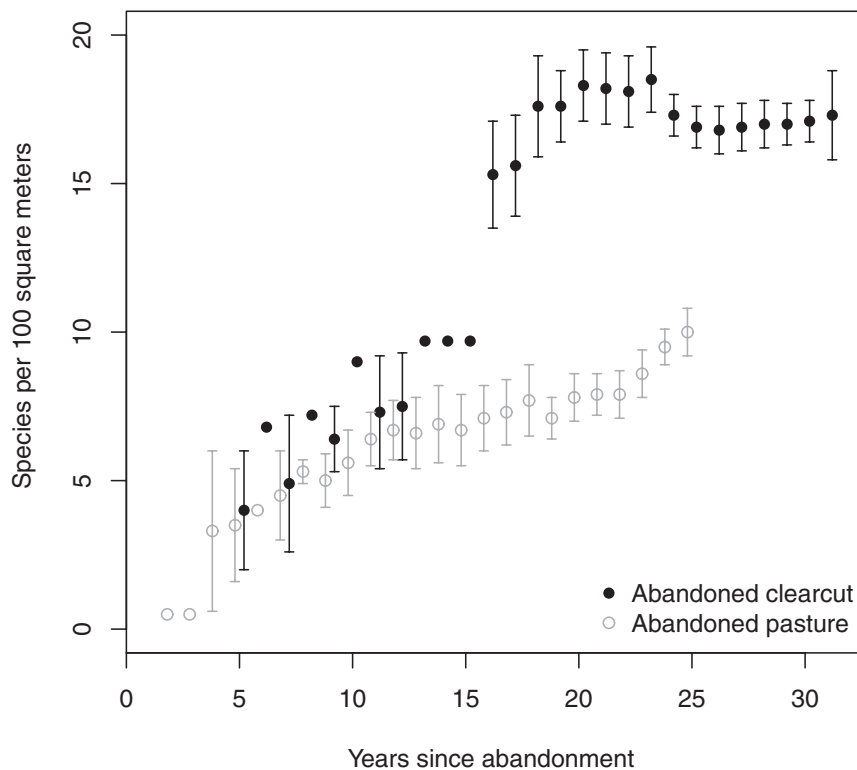


Figure 4. The number of species in 100-square meter transects of different ages in abandoned clearcuts (black circles) and abandoned pastures (gray circles). The error bars indicate the standard error.

Gomes and Luizao (2011) were unable to document significant differences in most cation concentrations between the *Vismia*-dominated and the *Cecropia*-dominated successions. Besides cations, available nitrogen might be affected by land-use history, because prescribed burning is known to release oxides of nitrogen. Gomes and Luizao (2011) found higher carbon-to-nitrogen (C:N) ratio in leaves of species growing on pastures when compared with those growing on clearcuts, indicating lower nutritional leaf quality, potentially derived from lower N availability in the soils. But they did not find significant effects for total nutrients at this site. However, it is well known that distribution of available N and phosphorus (P) in the organic, inorganic, plant-available, and insoluble fractions in the soil can change with land-use intensity (Runyan et al. 2012). We also tested for soil differences under *Vismia*- and *Cecropia*-dominated successions in the Apuí watershed about 1000 km south of the BDFFP and found that basal area, biomass, and species composition were independent of soil chemical and physical properties (box 1). Given the lack of consistency of independent studies across the Amazon, soil properties have not surfaced as the drivers of alternative successions, although further investigations based on nutrient flux may prove more fruitful.

After being abandoned, pastures are no longer burned, so differences with abandoned clearcuts might be expected to diminish over time. Plant assemblages on abandoned

pastures might converge on those in abandoned clearcuts, especially given the absence of physical and chemical differences in soils. However, instead of converging as succession unfolds, the communities continue diverging through time (figure 5, table 1, table 2; also shown by Williamson et al. 2014). By the second decade, *Cecropia*, as well as other short-lived pioneers, have largely ceded dominance to layers of regenerating secondary and old-growth forest species. No such transition occurred in pastures as *Vismia* remained dominant or shared dominance with one newcomer, *Bellucia*, over the 25 years of our study (Longworth et al. 2014).

These results suggest an important role for dispersal and colonization limitation in both the origin and maintenance of alternative successional sequences. Around our study sites, forest is still prevalent in the landscape, in contrast with some parts of the Amazon that are heavily deforested. At the BDFFP, seed sources and seed dispersers are available for both successional pathways, so distance to the forest is probably not limiting seed dispersal. Divergent

species composition in secondary forests, however, may importantly affect dispersal to these patches. *Vismia* trees might fail to attract the large birds and mammals that could introduce propagules from nearby primary forest species, which may help explain why *Vismia*-dominated pastures exhibit stubbornly slow succession. Abandoned clearcuts, in contrast, harbor primary forest stump sprouts and seedlings that survived deforestation; furthermore, the dominant colonizer, *Cecropia*, attracts a variety of birds and mammals (Estrada et al. 1984), thereby facilitating succession. To test the hypothesis of differential seed dispersal, Wieland and colleagues (2001) placed seed traps in both *Cecropia* and *Vismia*-dominated secondary forests. Both sets of traps captured many seeds, but nearly all of them were the very pioneer species already present in extant vegetation, not propagules from nearby mature forests. Indeed, the dispersal limitation of old-growth forest species seemed strong but not differentially prevalent in abandoned pastures versus abandoned clearcuts. Seedling emergence has been shown to depend on litter presence and light availability in clearcut areas, but seedlings emerging from seed banks are nearly exclusively pioneer species in abandoned pastures (Bentos et al. 2013), further reinforcing the seed dispersal limitation.

Under such strong dispersal limitation, species turnover is probably initially dependent on the seeds, seedlings, and sprouts left after disturbance. Although clearcuts had a diverse seed bank and sprout legacy, pastures had mainly

Bray–Curtis estimator basal area–based index

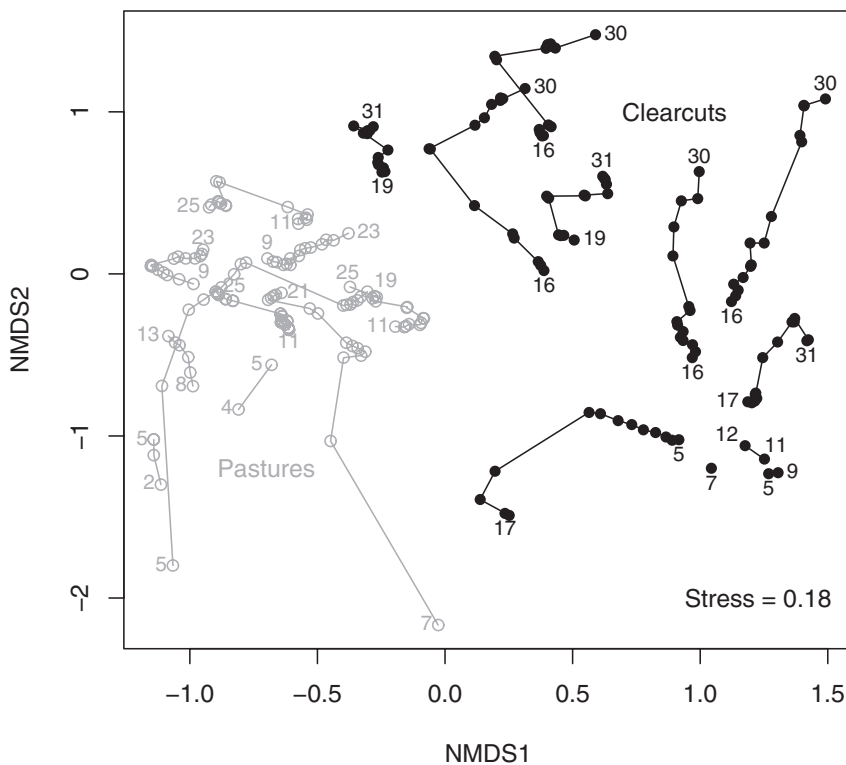


Figure 5. A nonmetric dimensional scaling (NMDS) ordination of floristic composition (individuals more than or equal to 3 centimeters diameter at breast height), with species weighted for basal area for the vegetation transects sampled through time for abandoned pastures (gray circles) and abandoned clearcuts (black circles). A transect sampled over a number of years is represented by connected lines, and the labels indicate the age of the first and last sample year, as of the fifteenth census in 2014. Transects that were sampled for a few or only one year were lost because of unplanned fires.

Vismia sprouts that survived prescribed burns. Repeated cutting and burning increases the dependency on strong sprouters over seed banks in early succession (figure 1; Jakovac et al. 2015). Thereafter, accumulation of species in these post-pasture secondary forests depended on dispersal from adjacent forests and successful seedling establishment. Therefore, the land-use legacy strongly explains the initial divergence of the successional trajectories, but other factors reinforce the maintenance of such divergence during the second and third decades after abandonment (figure 5, table 1, table 2). These factors seem to be interspecific interactions in which dominance by *Vismia* limits the establishment and growth of other species.

***Vismia* the competitor**

The dominant pioneer species in the study sites have very different colonization strategies. *Cecropia* has a thin crown at the top of a tall trunk, which appears to allow light to reach the strata below it (Williamson et al. 1998, Williamson and Mesquita 2001), whereas *Vismia* has a thick, layered

crown and a dense root mat loaded with mycorrhizae, suggesting it may be a potent competitor under poor soil quality (Williamson et al. 1998, Freitas 2005). Judged superficially, *Cecropia* would be a succession facilitator and *Vismia* a succession inhibitor, according to classical terminology (Connell and Slayter 1977); however, experimental tests are needed to determine the relative importance of competition and facilitation in these alternative successions.

In an *in situ* experiment, seedlings transplanted into the chronosequences of abandoned pastures and abandoned clearcuts showed different growth rates (box 2). Seedlings in the clearcuts grew faster in younger than in older stands, because available light levels in the understory declined with stand age (Jakovac et al. 2014). These results are consistent with succession theory, in which light levels are reduced as succession unfolds and the available light under the canopy drives species turnover through recruitment (Swaine and Whitmore 1988). In the abandoned pastures, seedlings not only grew slowly, but also their relative growth showed no difference by age of the pasture. After adult *Vismia* had established, the light levels reaching the understory changed very little and were higher than in the clearcuts, where vertical stratification was more prominent (Jakovac et al. 2014). The lack of a vertical stratification in *Vismia* stands may result in higher light availability than in *Cecropia* stands, where light is intercepted by several understory layers before reaching the ground.

Although the *Vismia* stands intercepted less incoming light, seedling growth was retarded, thereby suggesting that seedling growth is limited by other factors than light in *Vismia* stands. There is evidence that species of *Vismia* are exerting competition through the rhizosphere, perhaps for nutrients or water (Mazzochini 2010). Experiments to separate competitive effects among dominant plants and other successional species are the logical next step to improve our understanding of the relative importance of biotic interactions and environmental factors in these secondary forests.

Generalizing across the Basin

A quarter of a century of monitoring at the BDFFP has revealed that the pathway of secondary succession is strongly dependent on land-use history. Forests regenerating on old pastures accumulate biomass and species at rates

Table 1. The Euclidean distances among points in the nonmetric multidimensional scaling ordination (figure 5).

Euclidean distance	Pasture (n = 7)		Clearcut (n = 8)	
	Mean	Standard deviation (SD)	Mean	SD
Among initial points	1.26	0.78	1.04	0.53
Among final points	0.47	0.19	1.44	0.75
Between initial and final point	0.80	0.82	0.77	0.39

Note: For each land-use treatment (clearcut and pasture), distances were calculated among samples at the first year of monitoring (initial points), among samples at the last year of monitoring (final points), and between the first and final point of each transect monitored through time. Only transects monitored continuously for more than 13 years were included in the analysis (n = 15).

Table 2. The percentage of species composition explained by land-use treatments and successional age, resulting from a distance-based redundancy analysis (d-RDA).

Predictors	Overall explanation (%)	Contribution to explained variation (%)	pseudo-F	p-value
Treatment	37.7	72.9	141	.002
Age	8.9	17.2	38.6	.002
Treatment*Age	5.1	9.9	24.5	.002
Total explanation d-RDA	51.7	100		

Note: The percentage of explanation contributed by each factor (treatment: clearcut or pasture, successional age, and the interaction between age and treatment) to the overall species ordination as well as each factor contribution to the model's explained variation (contribution to explained variation). Associated pseudo-F and p-values were calculated by 499 permutations.

considerably slower than those on forest clearcuts without subsequent anthropogenic disturbance. To broaden our investigation geographically, we initiated vegetation surveys in five other watersheds in the Amazon Basin (data not shown here). In these watersheds, secondary vegetation was sampled on plots of different ages to construct chronosequences of succession under different land-use histories. Despite differences in biotic and abiotic characteristics of each watershed and in the form and intensity of land uses, the newly sampled areas have corroborated the results obtained at the BDFFP. For example, in Apuí, one of the watersheds located in the southeastern portion of the Basin (figure 2), successions on old pastures and on old agricultural fields exhibit different trajectories. Species richness and biomass accumulation are slower on areas of pastoral use relative to agricultural use. The differences in species assemblages on the Apuí plots parallel the differences in the BDFFP plots, as was shown by NMDS ordination—namely, the pasture plots lie to the right of the agricultural plots in Apuí, just as the pasture plots lie to the right of the clearcuts at BDFFP (figure 9, axis 1), reflecting that, in spite of the floristic differences between the two watersheds, the land-use trajectories are quite distinct. In a land-use intensity gradient, Manaus clearcut plots represent the least impact, followed by Apuí agricultural fields and then pasture in both regions. However, it is also noteworthy that the two regions are separated from each other on the second axis, reflecting differences in species composition between watersheds. The parallels between the various watersheds suggest that intensity of land use, especially the application of prescribed fire, may be the driver of the diverted successions.

Novel forests and ecosystem services

Resprouting by *Vismia* spp in pastures, shifting cultivation, and along roadsides clearly ensures its success in periodically burned and cutover habitats (Jakovac et al. 2015). However, given the recent proliferation of these anthropogenic processes, resprouting can hardly be considered an adaptation to repeated burning and clearing in the Amazon. More simply, *Vismia* appears to be one pioneer genus capable of surviving repeated burning, because Amazon trees are generally not well adapted to fires (Uhl and Kaufmann 1990). Such chance matching of a crucial trait with a new environment for the Amazon may have resulted from a historically advantageous trait in an ancestral line. A recent phylogeny of the Malpighiales clade (Ruhfel et al. 2011), which includes *Vismia*, shows closely related *Vismia* species in Africa and the Neotropics, indicating a Gondwanan distribution for the genus with its closest relative in Madagascar. So, resprouting from subterranean tissues after fire may be an ancestral trait evolved under a different fire regime prior to *Vismia* evolution as a rain forest pioneer (Gould and Vrba 1982). It is noteworthy that in forest treefall gaps (30 to over 400 square meters) where *Vismia* species regenerate, resprouting has not been observed, although cutting stems induces resprouting (Williamson et al. 1998). Now, *Vismia*, a widespread genus of pantropical trees common to disturbed habitats, is destined to become more abundant as pastures and roadsides replace rainforest throughout the Amazon and in Brazil's coastal rain forest (Williamson and Mesquita 2001).

Given the documented dynamics of turnover and the lack of tree species turnover or succession in *Vismia*-dominated sites, we question whether secondary succession processes will ever converge with those observed in other

Box 1. The life history of *Vismia*.

Seven *Vismia* species are known to occur in the BDFFP forests: *V. guianensis*, *V. cayenensis*, *V. japurensis*, *V. amazonica*, *V. macrophylla*, *V. bermeguii*, and *V. cauliflora*. Most *Vismia* species colonize forest edges, canopy gaps, roadsides, and pastures, with three species—*V. guianensis*, *V. cayenensis*, and *V. japurensis*—being abundant in secondary forests. In mature Amazonian forests, *Vismia* are canopy trees reaching 40 centimeters (cm) in diameter and 30 meters (m) in height. Their trunks are straight and solid, and the wood density is moderate (WSG = 0.45–0.53 grams per cubic centimeter).

In general, *Vismia* is a genus of classic pioneer species that respond to disturbance, because the plants are sun loving and show relatively high growth rates. In abandoned pastures and young secondary forests subject to regular pruning and fires, it is an aggressive colonizer capable of profuse resprouting and growth from lateral roots, forming clones after the loss of the main stem in surface fires (figure 6a; Williamson et al. 1998, Monaco et al. 2003). Rarely, if ever, do individuals show clonal growth inside mature forests. *Vismia*'s numerous small seeds are dispersed by generalist bats (Bobrowiec and Gribel 2009). The seeds germinate rapidly when dispersed into open areas, and they seem ever present in soil seed banks.

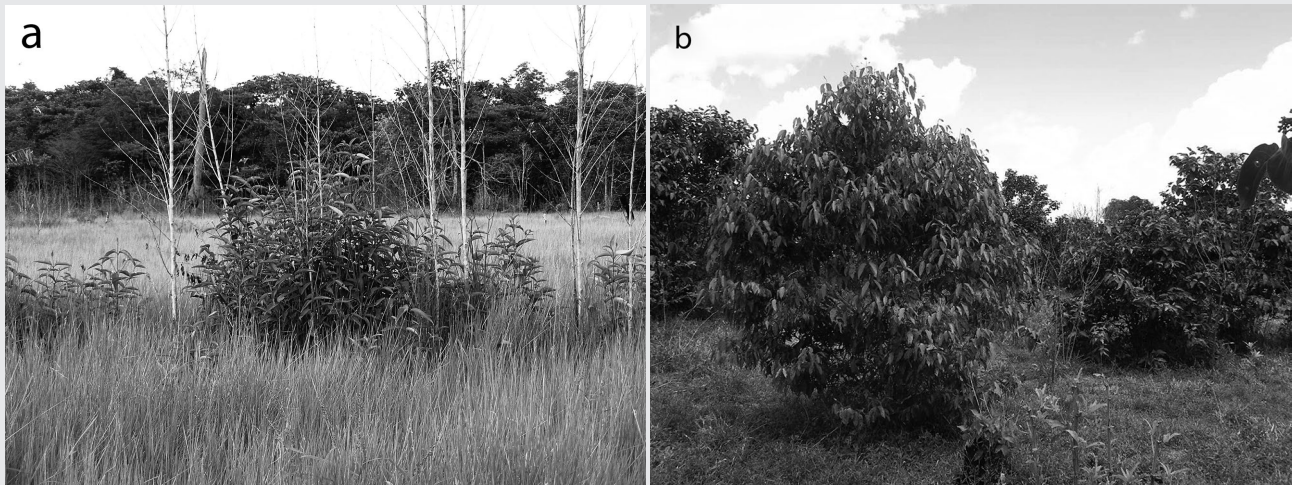


Figure 6. A *Vismia* plant at different stages of its life cycle: (a) resprouts after a pasture fire killed their 3-year-old stems (the dead standing trunks); (b) a cone-shaped *Vismia* crown during the early colonization of an abandoned pasture.

Vismia seems to be a successful inhibitor of the establishment of other species, and different factors may play a role in this inhibition. *Vismia* tree crowns are very dense, and once they are formed, their cone shape (figure 6b) intercepts much of the incoming sunlight, making the understory inhospitable for other pioneers.

In the central Amazon, where soils are old and very poor, many species form associations with mycorrhizae that improve their ability to uptake phosphorus and other significantly limiting soil nutrients. Freitas (2005) described 11 species of arbuscular mycorrhizal fungi associated with *Vismia japurensis* roots from our study sites. The competitive advantage that these associations provide for early plant establishment is still unexplored. Succession in abandoned Amazonian pastures is arrested because of initial floristics dominance by the genus *Vismia*, but how long *Vismia* will persist along successional time is unknown. After 25 years—and long after the human disturbances that fostered *Vismia* colonization—this remarkable genus remains the sole dominant of sites that were exposed to high-intensity use history (figure 7).



Figure 7. Twenty-year-old, even-aged stems in a *Vismia*-dominated second growth with its characteristic open understory.

Box 2. Local scale evidence for arrested succession in abandoned pastures.

In tropical forest succession, changing light availability is a key driver of species turnover (Swaine and Whitmore 1988): Fast-growing, light-demanding species are favored in early successional stages but are suppressed under low light levels in late succession, where slow-growing, shade-tolerant species are more competitive. Light availability at ground level decreases through succession as a result of increasing aboveground biomass, stratification, and canopy height (Chazdon et al. 2007). We evaluated how light availability and land use affected seedling growth in two chronosequences of abandoned pastures (*Vismia*-dominated succession) and clearcuts (*Cecropia*-dominated succession). We planted 990 seedlings of nine tree species (*Swietenia macrophylla*, *Dipteryx odorata*, *Carapa guianensis*, *Bertholletia excelsa*, *Copaifera multijuga*, *Hymenaea courbaril*, *Oenocarpus bacaba*, *Aniba rosaeodora*, and *Theobroma cacao*). We monitored height growth for 17 months (Jakovac et al. 2014). The seedling relative growth rate (RGR) differed by species, by successional type, and by light availability. Photosynthetically active radiation (PAR) in the understory, relative to full sunlight, was lower in the *Cecropia*-dominated succession (mean = 8.7%, standard deviation [SD] = 8.9) than in the *Vismia* chronosequence (mean = 14.7%, SD = 18.3). In addition, the rate of change in PAR with stand age followed different trends. The *Cecropia*-dominated succession showed the classical pattern of decreasing light availability with age, but in the *Vismia*-dominated succession, light availability didn't change after passing an initial threshold. As a consequence, the RGR decreased with increasing stand age in the *Cecropia* succession but did not vary with age in the *Vismia* succession. Furthermore, when controlling for the effect of stand age, increasing the PAR resulted in a higher RGR in the *Cecropia* succession but not in the *Vismia* succession. Under a light gradient varying from 0% to 90% of PAR, the RGR of *C. guianensis*, for example, increased threefold (300%) in *Cecropia* stands but did not surpass 1% in *Vismia* stands (figure 8). Nutrient limitation or belowground competition with the dominant well-rooted *Vismia* species could be playing a role in limiting seedling growth, but further research is needed to disentangle these factors. The higher light availability in the *Vismia* understory compared with that in *Cecropia* stands may favor pioneer over shade-tolerant species and could partially explain the low species turnover found in abandoned pasturelands (Norden et al. 2011, Longworth et al. 2014)

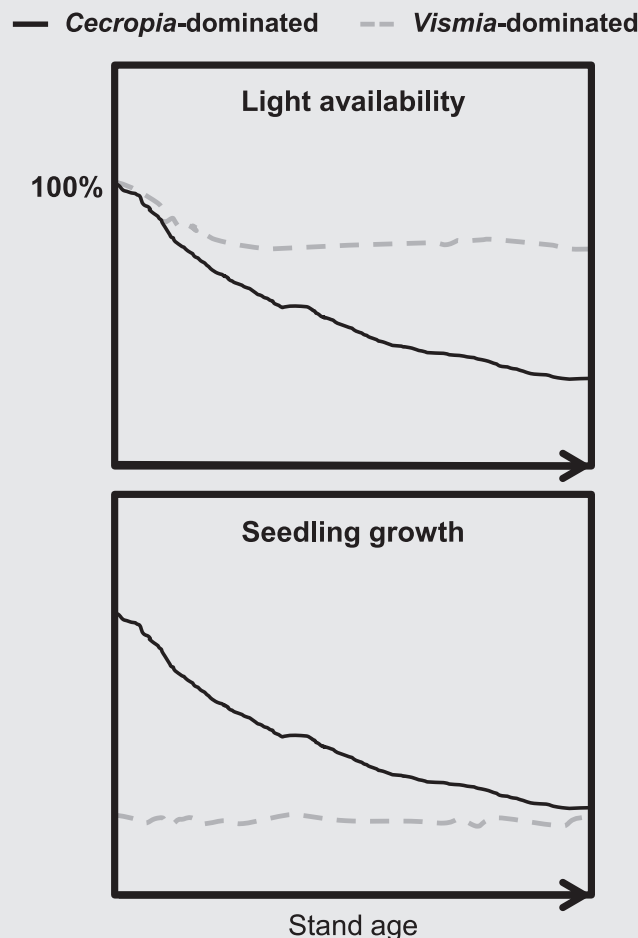


Figure 8. A schematic description of the variation in light availability and seedling growth rates with stand age for *Vismia* and *Cecropia* stands.

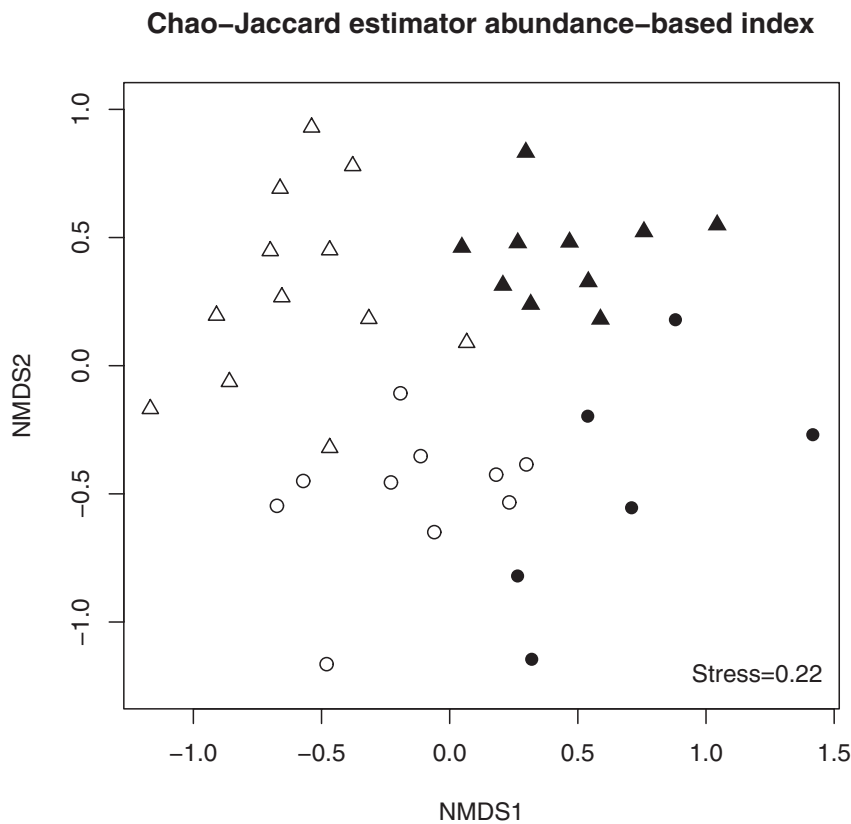


Figure 9. A nonmetric dimensional scaling (NMDS) ordination of the floristic composition in secondary forests in Apuí (circles) and Manaus (triangles). The solid symbols represent plots inventoried in former pasturelands, and the open symbols show the clearcut plots in Manaus and plots previously cultivated for agriculture by smallholders in Apuí.

non *Vismia*-dominated sites. At least during the first 25 years of succession, *Vismia* has maintained high dominance in the sites where it was the initial dominant (Norden et al. 2011, Longworth et al. 2014). In anthropogenically altered ecosystems, emergent successional pathways may engender reorganized plant assemblages that after time converge on the prior community or alternatively diverge into unusual stable configurations (Suding et al. 2004). Some cases of the latter have generated novel forests, in part owing to introduced species, as in the tropical assemblages of Puerto Rico (Lugo 2012). Islands, of course, are notoriously prone to invasion, but even expanses of mainland tropical forests have exhibited transitional associations, such as during the Pleistocene. In modern times, climax forests may experience such “ecological fitting”—the expansion or contraction of a species’ distribution and the concomitant ecological adjustments by sympatric species without evoking evolutionary change (Janzen 1985). Over the last several decades, as a result of modern anthropogenic impacts and land-use intensification, the secondary forests of the Amazon Basin have been accommodating resprouting species at the expense of non-resprouting taxa. As the ecological fitting unfolds, large-scale, long-term monitoring provides both documentation

of such changes and the basis to develop and test hypotheses of the drivers of these alternative successional processes.

Under the current scenario of increasing land-use intensity in the Amazon Basin, it is likely that *Vismia*-dominated secondary forests will expand (Jakovac et al. 2015). Therefore, the reputed value of secondary forests for biodiversity conservation and as the providers of ecosystem services must take into account the different types of secondary forests originating from distinct land-use intensities and may therefore be questionable. Estimates of the carbon sequestration, useful-species availability, and conservation value of these secondary forests are based on succession following low-impact natural disturbances, not the alternative that occurs with the diverted succession following high-impact human activities uncovered here. Currently, there are no reliable estimates of the quality of the different types of secondary forests covering the 150,000 square kilometers of the Brazilian Amazon in terms of the ecosystem services they may or may not offer (Embrapa and INPE 2011). Therefore, extra effort should be devoted to improve our understanding of the predictability of secondary successional trajectories and the estimate of their value as ecosystem-service providers.

The replication and scale of successional trajectories

In a landscape littered with various anthropogenic elements, alternative assemblages of the same age may exist alongside an old-growth forest community—an apparent contradiction to the successional concept. One key to discerning different successional trajectories is replication of the treatments, which includes accurate information on prior land-use histories. Without large, well-replicated treatments, the successional dynamics would be judged as unpredictable, stochastic, or uncertain. For example, if we did not know the land-use histories of our plots, then the variation between the abandoned pastures and the clearcuts would be attributed to high stochasticity. Whereas different land-use histories produced different successional sequences, variability in stem density and species composition at a given age was evident within treatments—more so in the abandoned pastures than in the clearcuts (evident in figure 5). For the moment, such variability remains unexplained. Some of the excess variability in abandoned pastures might be the result of greater variation in land-use history, because pastures were used for different lengths of time, and when burned, fire intensity and frequency were somewhat irregular at the

farm scale, although we considered them one treatment vis-à-vis clearcuts. Small differences in the number of burning events strongly determine stem density, basal area, and canopy height (Zarin et al. 2005, Lawrence et al. 2010, Jakovac et al. 2015). Further unexplained variation undoubtedly rests in dispersal limitation (Robiglio and Sinclair 2011), recruitment timing, and biotic interactions under weather anomalies.

Amazonian successional sequences are complex in part because of extreme species richness but also because of the extreme variability in anthropogenic use before land is abandoned. In a few earlier studies of tropical rainforests, close attention to the selection of sites with a common land-use history resulted in relatively predictable successional attributes (Peña-Claros 2003), whereas in numerous others, stochasticity has been evoked to account for inexplicable assemblages (Norden et al. 2015).

Scale has been invoked recently as the cause for different results in studies of species assemblages in old-growth tropical rain forests: Stands that appear random assembled at small scales appear niche assembled at large scales (Garzon-Lopez et al. 2014). In parallel, studies of succession may suggest random assemblages at small scales and predictable community replacements at large scales (Bazzaz 1996). For tropical rain forest with hundreds of tree species and a plethora of anthropogenic land uses on small scales, the interpretations of forest regeneration may have been pushed inappropriately in the direction of stochasticity. In contrast, in our study, where land-use history was limited to two replicated treatments, succession appears more deterministic along two alternative pathways corresponding to prior land uses.

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