

Shifts in Dominance and Species Assemblages over Two Decades in Alternative Successions in Central Amazonia

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ABSTRACT

Following perturbation, different assemblages that originate under the same abiotic conditions initiate successional pathways that may continue to diverge or converge toward an eventual climax. Forest regeneration in the Central Amazon begins with alternative successional pathways associated with prior land use. In a 12-yr study of secondary forests, initially ranging between 2 and 19 yrs after abandonment, we compared species compositions through time along two pathways, abandoned clear-cuts dominated by *Cecropia* and abandoned pastures dominated by *Vismia*; prior results at these sites have not directly evaluated species composition. At all ages, the Chao–Jaccard similarity index of species composition was highest comparing pasture transects to each other, lowest comparing pastures transects to clear-cut transects, and intermediate comparing clear-cut transects to each other. Through time, clear-cut transects became less similar to each other, as did pasture transects. Changes in similarity reflected declining dominance along both pathways, but *Cecropia* dominance of clear-cut transects declined more rapidly than *Vismia* dominance of pasture transects. A rich association of species replaced *Cecropia* in clear-cut transects, resulting in decreased similarity among them. In pasture transects one genus, *Bellucia*, replaced the lost *Vismia*, so similarity of *Vismia* transects was maintained despite some turnover in dominance. Overall, even with turnover of individuals and decline of the dominant pioneers, the alternative pathways exhibited strikingly different species assemblages after two decades of succession, suggesting that the effect of land use persists well beyond initial floristic composition.

Abstract in Portuguese is available in the online version of this article.

Key words: basal area; *Cecropia*; forest regeneration; secondary succession; species density; stem density; *Vismia*.

DIFFERENT SPECIES ASSEMBLAGES SOMETIMES OCCUR IN THE SAME REGION under the same abiotic conditions. Initial floristic differences may result from stochasticity in species colonizations, or from differential perturbations of the original community. For example, alternative plant communities sometimes develop on adjacent sites exposed to altered fire regimes (Williamson *et al.* 1991, D'Odorico *et al.* 2006, Hoffmann *et al.* 2009, Martin & Kirkman 2009, Odion *et al.* 2010). Disturbances may also facilitate establishment of invasive species, thereby initiating new species assemblages (Knoop & Walker 1985, Bush & Van Auken 1989, D'Antonio & Vitousek 1994). Anthropogenic modification of the environment associated with the introduction of exotics and extirpation of natives frequently engenders new species assemblages that develop alternative successional pathways (Lugo 2012). Alternative pathways are evident in old-field successions, where prior land use influences initial community composition (Wong *et al.* 2010), frequently because recruitment is limited by seed dispersal and habitat fragmentation (Suding *et al.* 2004, Young *et al.* 2005).

Disturbances in the central Amazon Basin produce alternative successional pathways. Prior land use leads to strikingly

different pioneer assemblages when land is abandoned (Mesquita *et al.* 2001). Most commonly, forest clear-cuts are converted to cattle pastures that are subsequently abandoned within 6–8 yrs when they become unproductive (Fearnside 2005). Less commonly, land is abandoned immediately after deforestation. Abandoned clear-cuts develop a canopy dominated by the pioneer genus *Cecropia* (*C. sciadophylla*, and *C. purpurascens*), characterized by a diverse understory of seedlings and saplings of primary forest species. In contrast, abandoned pastures develop nearly monogeneric stands of *Vismia* (*V. cayennensis*, *V. guianensis*, and *V. japurensis*) with poor representation of mature forest species in the seedling layer (Uhl *et al.* 1988, Mesquita *et al.* 2001, Williamson & Mesquita 2001). The initial compositional difference may be explained by grazing and the use of prescribed fires in pastures, as *Vismia* is a prolific resprouter relative to other rain forest trees, most of which are killed by fire (Kauffman 1991). Within a few years after abandonment, clear-cuts succeed toward primary forest much like regeneration in forest gaps, whereas pastures change more slowly, accumulating fewer species (Uhl *et al.* 1988, Mesquita *et al.* 2001, Norden *et al.* 2011).

Here we use 12 yrs of vegetation censuses from sites of various ages to determine if species compositions on abandoned clear-cuts and abandoned pastures are becoming more similar through time and whether the dominant genera are declining.

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Communities might become more similar over time if there is sufficient turnover of individuals and if new recruits are less dependent on prior land use than are early colonizers. High stem turnover without convergence of the species assemblies may reflect ongoing effects of initial floristics together with prevailing site effects such as dispersal limitation or soil differences. In an earlier study, we documented that two stand characteristics, stem density and basal area, tended to converge after two decades of succession, but a third trait, species density, diverged over the same time period (Williamson *et al.* 2014). We also previously documented that for the first 8 yrs, tree turnover was faster in stands on abandoned clear-cuts than in stands on abandoned pastures (Norden *et al.* 2011). These previous studies have not directly compared species composition. Now, we direct attention to taxonomic identities to ascertain if species assemblies are becoming more similar through time. Given that stem densities and basal areas tend to converge, but species richness diverges, species assemblies could be converging toward a common composition, or the assemblage from one treatment could converge on the other, or they may remain dissimilar through time.

METHODS

STUDY SITE.—This study was conducted 80 km north of Manaus, Brazil (2°30'S, 60°W), in the reserves of the Biological Dynamics of Forest Fragments Project (BDFFP). Average annual rainfall in

Manaus is 2.2 m, with a mild dry season between July and November (Satyamurty *et al.* 2010). Mean annual temperature is 26°C. The soils are nutrient poor, clay-rich oxisols, predominantly red-yellow podzols and yellow latozols (Ranzani 1980). The dominant vegetation is dense evergreen *terra firme* forest.

The BDFFP study areas were deforested in the early 1980s, creating three large farms on which fragments of primary forest were retained for further investigation. Maps and land use histories have been previously published (Moreira 2003, Laurance *et al.* 2011, Norden *et al.* 2011). Some portions of the cleared farms were abandoned shortly after deforestation, whereas others were converted to pasture, burned annually, grazed, and subsequently abandoned 6–8 yrs later. The two different land use types, abandoned clear-cuts versus abandoned pastures (Table 1), led to different types of forest regeneration; areas subjected to little or no prescribed burning or grazing became dominated by the genus *Cecropia*, about 45 percent of stems after 10 yrs, whereas areas burned regularly and grazed were dominated by *Vismia*, about 70 percent of stems after 10 yrs (Mesquita *et al.* 2001). Most of the region around the PDBFF reserves is still primary forest.

VEGETATION SAMPLING.—From 1999 to 2003, we established 22 belt transects in secondary forests ranging from 2 to 19 yrs since abandonment (Table 1). Of the 22 transects, 12 were dominated by *Cecropia*, all of which were abandoned clear-cuts, and 10 by *Vismia*, all of which had been converted to pasture for 6–8 yrs.

TABLE 1. Summary information for vegetation transects. Shaded transects were lost to wildfires.

Location of transect	Land use	Age during study	# of fires	Initial dimensions	Final dimensions	Number of surveys	Years surveyed
P. Alegre	Clear-cut	5	2	100 × 6 m	100 × 6 m	1	2000
P. Alegre	Clear-cut	5–15	2	100 × 6 m	100 × 6 m	11	2000–2011
ZF-7	Clear-cut	7	1	50 × 6 m	50 × 6 m	1	2002
ZF-7	Clear-cut	9	1	50 × 6 m	50 × 6 m	1	2002
ZF-7	Clear-cut	11–12	1	50 × 6 m	50 × 6 m	2	2002–2003
Florestal	Clear-cut	16–27	0	100 × 3 m	100 × 5 m	12	1999–2011
Florestal	Clear-cut	16–27	0	100 × 3 m	100 × 5 m	12	1999–2011
P. Alegre	Clear-cut	16–27	0	100 × 3 m	100 × 5 m	12	1999–2011
P. Alegre	Clear-cut	16–27	0	100 × 3 m	100 × 5 m	12	1999–2011
Dimona	Clear-cut	17–28	0	100 × 3 m	100 × 5 m	12	1999–2011
C. Powell	Clear-cut	19–28	0	100 × 3 m	100 × 5 m	10	2002–2011
C. Powell	Clear-cut	19–28	0	100 × 3 m	100 × 5 m	10	2002–2011
Dimona	Pasture	2–5	9	75 × 5 m	75 × 5 m	4	1999–2003
Colosso	Pasture	4–5	5	100 × 1 m	100 × 1 m	2	1999–2000
Dimona	Pasture	5–16	7	100 × 1 m	100 × 5 m	12	1999–2011
Dimona	Pasture	7–18	5	100 × 1 m	100 × 5 m	12	1999–2011
Km 17	Pasture	8–13	6	100 × 2.5 m	100 × 2.5 m	6	1999–2005
Dimona	Pasture	9–20	4	100 × 2.5 m	100 × 5 m	12	1999–2011
Florestal	Pasture	9–20	4	100 × 5 m	100 × 5 m	12	1999–2011
Cabo Frio	Pasture	11–22	2	100 × 2 m	100 × 5 m	12	1999–2011
Cabo Frio	Pasture	11–22	2	100 × 2 m	100 × 5 m	12	1999–2011
Colosso	Pasture	11–22	3	100 × 5 m	100 × 5 m	12	1999–2011

For both *Vismia* and *Cecropia* stands, transects were chosen to represent different ages of succession, based on written site history confirmed by remotely sensed images (Moreira 2003). Also, the number of prescribed burns after each clear-cut was determined (Table 1). We monitored vegetation annually through 2011. Seven transects—four dominated by *Cecropia* and three by *Vismia*—were lost to wildfires 1–6 yrs after their initial censuses.

We chose transects to provide variability in successional ages. As the treatments (clear-cuts vs pasture conversions) occurred in large blocks on each farm and the three farms were separated by about 20 km on an east-west line, there was the potential for spatial autocorrelation among treatments. However, transects of both treatments were spread across the east-west continuum (Fig. S1). Generally, the two treatments were highly intermingled, so spatial autocorrelations are unlikely (Norden *et al.* 2011). By our own analysis there were only very weak relationships between Chao–Jaccard similarity and distance between sites (similarities from the 22 first year surveys of various ages: $R^2 = 0.0008$, $F_{1,230} = 0.19$, $P = 0.66$; similarities from the 15 surveys of 19-yr-old transects: $R^2 = 0.0003$, $F_{1,65} = 0.02$, $P = 0.88$). In order to capture data on the early years of succession, we established three transects on roadside clear-cuts between the two easternmost ranches, Porto Alegre and Esteio (Fig. S1), which were sampled initially, but lost to fires after the first or second census. Plots analyzed here were identical to those in Williamson *et al.* (2014). Norden *et al.* (2011) used the first eight censuses on the same plots plus several plots in abandoned manioc and rubber plantations that were excluded both in this study and in Williamson *et al.* (2014).

In most cases, transects were 100 m long, but four were shorter, either 50 m or 75 m as a result of stand shape. Initially transect widths ranged from 1 m to 6 m such that older transects with fewer stems were wider. In 2008, the width of all transects whose areas were less than 500 m² were expanded to make each transect 500 m² (Table 1).

In each annual census we determined the diameter at breast height (dbh) and taxonomic identity of each stem in a transect. For our analysis we only used stems ≥ 3 cm. As plots had been clear-cut and/or burned, recruitment included some individuals with multiple stems originating at the base or root crown of killed stems. *Vismia* species are known to resprout prolifically from lateral roots after death of the main stem (Williamson & Mesquita 2001). We treated stems that were separated by at least 10 cm as separate individuals, whereas those separated by less than 10 cm were considered multi-stemmed individuals. For multi-stemmed individuals, we recorded the dbh of each stem and basal areas combined. We identified nearly all individuals to species or morphotyped to genus, although a few were morphotyped only to family.

We conducted censuses annually in the dry season of the first 2 yrs (August of 1999 and 2000), and subsequently in the rainy season between February and April of 2002–2011. Thus, the interval between censuses was roughly 1 yr except the 2000–2002 interval, which was one and a half years. For analyses here, we treated each census interval as 1 yr. At each census, we identified and measured new individuals that recruited into the

appropriate size class for each transect, and re-measured remaining individuals.

SIMILARITY.—To measure similarity in species composition, we calculated the Chao–Jaccard similarity index, for each pair of transects of the same age. This index, calculated with the EstimateS software package, estimates the similarity of two samples based on abundances, in our case using number of stems not individuals, and corrects for unseen species (Chao *et al.* 2005). We grouped transect pairs by treatment—pastures or clear-cuts—and then determined pairwise means for each treatment-age transect combination. Mean similarities were produced for ages 10–22 yrs after abandonment of pastures and ages 10–28 yrs after abandonment of clear-cuts. We treated the period from 5 to 9 yrs as a single age, 7 yrs, because there were few comparisons for that period.

Mean similarity for pairs of abandoned clear-cut sites (C-C), for pairs of abandoned pasture sites (P-P) and for pairs of clear-cut sites and pasture sites (C-P), together reveal whether sites with the same land use history were more similar than sites with different histories at each age. We used linear regressions, or exponential regressions when appropriate, to determine the effect of age on mean similarity for each comparison type (C-C, P-P and C-P)—namely how similarity changed through successional age. In addition, we constructed a non-metric dimensional scaling of all years on one plot using the Chao–Jaccard similarities.

To provide more detailed composition information for 20-yr-old transects, we compared the Chao–Jaccard index by land use (C-C, P-P, C-P) for two different size classes: large trees (≥ 10 cm dbh) and small trees (3–10 cm dbh). Likewise, we calculated similarities for the cohort of trees recruited (growing into the ≥ 3 cm dbh class) during the interval of 17–22 yr, for a corresponding comparison to the two stem size classes at 20 yr. (Recruitment in the age 20 yr was too small to be meaningful, so we employed the interval 17–22 yr). These three groups potentially represent the future successional stages (Van Breugel *et al.* 2007), therein allowing a preview of how similarities would change in the coming years for different land uses. A single-factor ANOVA with Tukey pairwise comparisons was used to examine the impact of land use (C-C, P-P, C-P) on similarity separately for each stage class. Likewise, the similarity of the overstory (stems ≥ 10 cm) to the understory (stems < 10 cm) was compared at 20 yrs to project possible future changes in composition for both land use histories.

DOMINANCE.—We performed three analyses of dominance. First, we calculated the proportions of basal area and of stems of the initial dominant genera, *Cecropia* in clear-cuts and *Vismia* in pastures, each year for each transect and then averaged for all transects of each land use at each age. The proportion of basal area was also calculated for the genus *Bellucia* in both land uses since it was noted as a later dominant. To statistically test the trend in dominance through time, we performed an ANCOVA on the arcsine-square-root transformed proportions with age as the covariate and land use history as the independent variable.

To determine whether there was a difference in the rate of decline of the dominant species, we tested the significance of the interaction term of stand type with age (age*stand) in the model. Only if the interaction term was not significant was the effect of the stand type term (stand) on dominance examined. We performed the ANCOVA on a chronosequence, which ranged from 5 to 22 yr for both land uses, that included only the fourth year of each clear-cut transect and the final year of each pasture transect. We used different years because abandoned pastures were younger than abandoned clear-cuts, as both were deforested in the same year. The chronosequence was used instead of every year for every transect to avoid inflating the degrees of freedom through repeated measures. Second, to view the change in the dominant pioneer populations over time, we constructed the size class distributions (3–5 cm, 5–10 cm, 10–15 cm, 15–20 cm, >20 cm) separately for *Cecropia* from abandoned clear-cuts and for *Vismia* from abandoned pastures with data from all transects at two ages, 9 and 22 yr. We created average size class distributions by proportion of stems in each size class for four categories: 9-yr-old pastures, 9-yr-old clear-cuts, 22-yr-old pastures, 22-yr-old clear-cuts. Third, we examined newly dominant species 20 yr after abandonment for transects that were at least that old or at the most recent survey for those not yet 20-yr-old. Newly dominant species means those species besides *Vismia* for abandoned pastures and *Cecropia* for abandoned clear-cuts, which were most dominant by proportion of basal area in each transect.

TURNOVER RATES.—We calculated stem gain (recruitment) and stem loss (mortality) as the percent of stems lost or gained per year in each transect for all species combined. As sample sizes were limited, we aggregated recruitment and mortality separately for three periods: 3–9, 10–16 and 17–22 yrs. We compared average rates per transect in clear-cuts versus pastures with *t*-tests for the 17–22 yr period, which had similar sample sizes ($n_{\text{Pastures}} = 6$, $n_{\text{Clear-cuts}} = 7$) and with the non-parametric Mann–Whitney tests for the 10–16 yr period, which had unequal replication ($n_{\text{Pastures}} = 8$, $n_{\text{Clear-cuts}} = 2$). We did not compare recruitment and mortality at 3–9 yr as we only had a sample of one transect for clear-cuts. In addition, we compared recruitment and mortality of the initially dominant genera from each site, *Cecropia* or *Vismia*, for the 17–22 yr period.

RESULTS

SIMILARITY.—The mean Chao–Jaccard similarity of 7-yr-old transects was higher in abandoned pasture (0.62 ± 0.04) than in clear-cut sites (0.40 ± 0.02) (Fig. 1). Furthermore, abandoned clear-cuts and pastures were very different from each other (0.25 ± 0.02) (Fig. 1). Through time all of the similarities decrease, and at 22 yr pasture sites remain more similar to other pasture sites (0.40 ± 0.06) than to clear-cut sites (0.15 ± 0.01). Clear-cuts sites are also more similar to each other (0.20 ± 0.01) than to pasture sites. An NMDS ordination of these similarity values reflects these trends (Fig. S2).

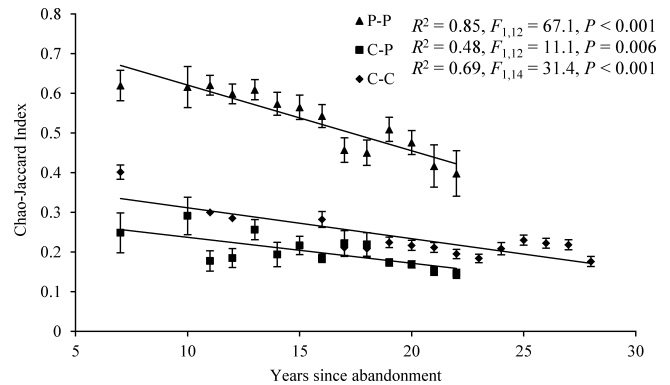


FIGURE 1. Successional change in the mean Chao–Jaccard similarity index for abandoned clear-cuts (C-C) with each other, abandoned pastures (P-P) with each other and clear-cuts with pastures (C-P).

Land use history also had a significant effect on Chao–Jaccard similarity when size classes were examined separately in 20-yr-old transects (Appendix S1 contains statistical tests). Pasture sites (P-P) were the most similar to each other in both the largest size class of stems ≥ 10 cm dbh and in the 3–10 cm dbh size class (Fig. 2A). Clear-cut sites (C-C) were more similar than pastures and clear-cuts (C-P) in the 3–10 cm dbh size class but not in the ≥ 10 cm dbh. For individuals recruited between 17 and 22 yr there was also an effect of land use. While the similarity in pastures (P-P) and clear-cuts (C-C) was not significantly different, these recruits were significantly more similar in sites of the same land use history (C-C and P-P) than in sites with a different land use history (C-P). Furthermore, the similarities tended to decline from stem class ≥ 10 cm to stem class 3–10 cm to new recruits, indicating that transects of a given comparison (C-C, P-P or C-P) became more dissimilar through time.

Possibly reflecting the future also was the overstory-understory comparison. In 20-yr-old transects, the understory was more similar to the canopy in abandoned pastures than in abandoned clear-cuts (Fig. 2B; $t = 4.17$ df = 5 $P = 0.009$).

DOMINANCE.—All young transects were dominated by either *Cecropia* or *Vismia* species. Twenty years after abandonment the single most dominant species, excluding the dominant pioneer genus, varied among seven different species and genera in the eight clear-cut transects but among only three different species and two genera in the seven pasture transects (Table 2). At this age, more pasture transects were still dominated by *Vismia* (6 of 7) than clear-cut transects were dominated by *Cecropia* (3 of 8).

Dominance by *Cecropia* and *Vismia* decreased during the first three decades of succession (Fig. 3). The chronosequence data (not shown) revealed that the proportion of basal area of *Cecropia* in clear-cuts decreased more rapidly than the proportion of basal area of *Vismia* in pastures (ANCOVA: age*stand, $F_{1,18} = 4.77$ $P = 0.042$). In terms of proportions of stems (Fig. 3B), the rate of decline in dominance was the same in both pioneers (age*stand, $F_{1,18} = 1.27$, $P = 0.27$) despite *Cecropia* being less

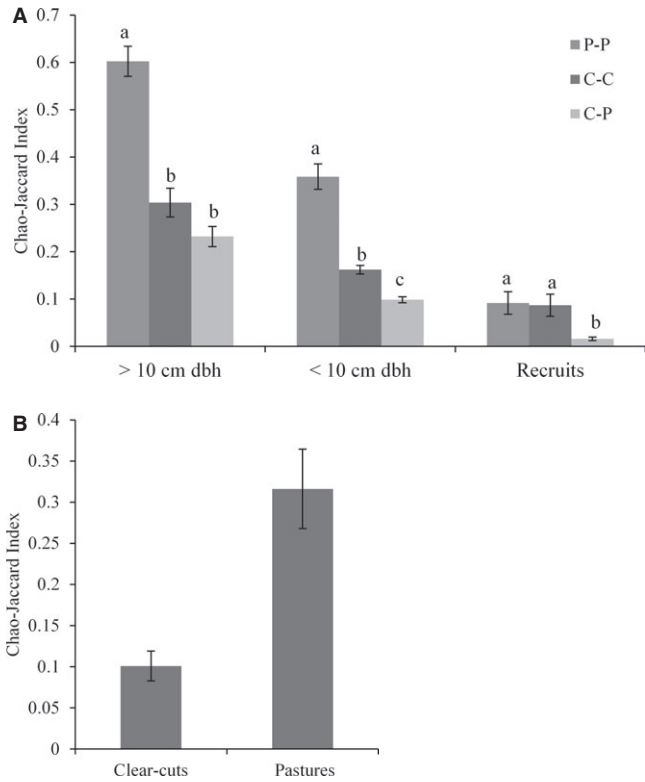


FIGURE 2. Chao-Jaccard similarities based on different size classes. (A) Mean (\pm SE) Chao-Jaccard similarity index weighted by number of stems in 20-yr-old transect treatments of abandoned pastures only (P-P), abandoned clear-cuts only (C-C) and both pastures and clear-cuts (C-P). Different letters indicate significant differences within size classes ($P < 0.05$). Differences among size classes were not tested. Appendix A shows statistical results. (B) Mean (\pm SE) Chao-Jaccard similarity index weighted by number of stems and comparing the species composition of the overstory (stems ≥ 10 cm) to the species composition of the understory (stems 3–10 cm) at each 20-yr-old transect of two land use histories.

dominant overall (stand, $F_{1,18} = 27.12$, $P < 0.001$). *Bellucia* dominance increased in pastures (25% of basal area by 22 yrs) but remained low in clear-cuts (3% of basal area at 22 yrs).

The size class distributions of the dominant genera showed that *Cecropia* in clear-cut transects had a greater proportion of large individuals (≥ 10 cm dbh) than *Vismia* in pasture transects at both 9 and 22 yr (Fig. 4). Also, the aging of the *Cecropia* population, which had no small individuals (< 10 cm dbh) at 22 yr, occurred much more rapidly than the *Vismia* population, which contained approximately 50 percent of small individuals at 22 yr.

TURNOVER RATES.—Recruitment was not significantly different between clear-cut and pasture transects from 10–16 yr (Mann-Whitney $U = 7$, $P = 0.44$; Fig 5A) or from 17–22 yr ($t = 0.266$, $df = 11$, $P = 0.397$). Mortality in clear-cuts was significantly higher than in pasture transects from 10–16 yr (Mann-Whitney $U = 1$, $P = 0.044$; Fig. 5B), but from 17–22 yr mortality was significantly lower in clear-cut transects ($t = 3.97$, $df = 11$,

TABLE 2. Dominant species by proportion of basal area at 20 yrs or in the most recent survey (2011), excluding the initially dominant genera (*Cecropia* or *Vismia*). Shaded transects are those in which the species listed is more dominant than all of the *Cecropia* or *Vismia* species combined. Note that a *Vismia* or *Cecropia* species can be the dominant after excluding *Cecropia* spp. from clear-cut transects (transect 23) and *Vismia* spp. from pasture transects (transect 4), respectively. This table does not include the seven transects lost to fire.

Transect #	Land Use	Age	Dominant species other than <i>Cecropia</i> or <i>Vismia</i>	Proportion of basal area	<i>Cecropia</i> or <i>Vismia</i> proportion of basal area
6	Clear-cut	20	<i>Simarouba amara</i>	0.16	0.15
7	Clear-cut	20	<i>Pourouma tomentosa</i> subsp. <i>apiculata</i>	0.15	0.06
12	Clear-cut	20	<i>Byrsonima duckeana</i>	0.10	0.42
13	Clear-cut	20	<i>Guatteria olivacea</i>	0.14	0.32
17	Clear-cut	20	<i>Croton lanjouvensis</i>	0.09	0.33
21	Clear-cut	15	<i>Inga thibaudiana</i>	0.13	0.01
22	Clear-cut	20	<i>Croton lanjouvensis</i>	0.25	0.06
23	Clear-cut	20	<i>Vismia cayennensis</i>	0.20	0.05
1	Pasture	20	<i>Bellucia imperialis</i>	0.24	0.39
3	Pasture	20	<i>Bellucia imperialis</i>	0.18	0.41
4	Pasture	20	<i>Cecropia sciadophylla</i>	0.20	0.32
5	Pasture	20	<i>Bellucia grossularioides</i>	0.21	0.27
14	Pasture	16	<i>Bellucia imperialis</i>	0.20	0.51
15	Pasture	20	<i>Bellucia imperialis</i>	0.49	0.36
16	Pasture	18	<i>Bellucia imperialis</i>	0.06	0.70

$P = 0.002$). From 3–9 yr turnover rates were not compared statistically because $N = 1$ for clear-cuts; however, recruitment visually appeared to be much higher in pastures and mortality was higher in clear-cuts.

There was no recruitment of *Cecropia* stems in clear-cuts and very low recruitment of *Vismia* stems in pastures (0.375 stems/500 m^2 /yr; not shown) during the ages 17–22 yr. Percent mortality was not significantly different for *Cecropia* stems in clear-cuts and *Vismia* stems in pastures (*Cecropia* = 0.12, *Vismia* = 0.10, $t = 0.497$, $df = 11$, $P = 0.63$; not shown).

DISCUSSION

The purpose of this study was to determine whether species composition of two successional pathways became more similar over time. Turnover in dominant species and turnover in stems in the pathways were compared to explain the trends in similarity over time. In addition, similarity of the smallest size classes was examined separately to predict whether the pathways would converge in the future.

Are the two successional pathways converging on one another, maintaining differences or diverging? Convergence might

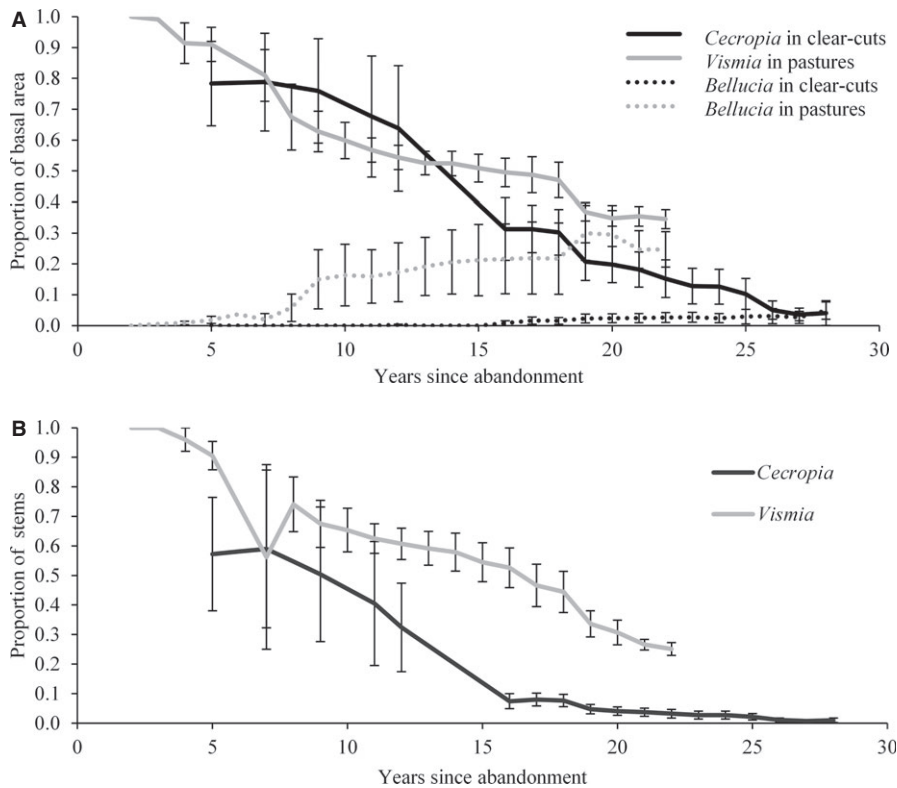


FIGURE 3. Mean (\pm SE) proportion of basal area (A) and stems (B) comprised by the dominant genera of plants in abandoned clear-cuts (*Cecropia*) and abandoned pastures (*Vismia*) during the first three decades of succession. (A) includes the proportion of basal area of the genera *Bellucia* for both types of land use.

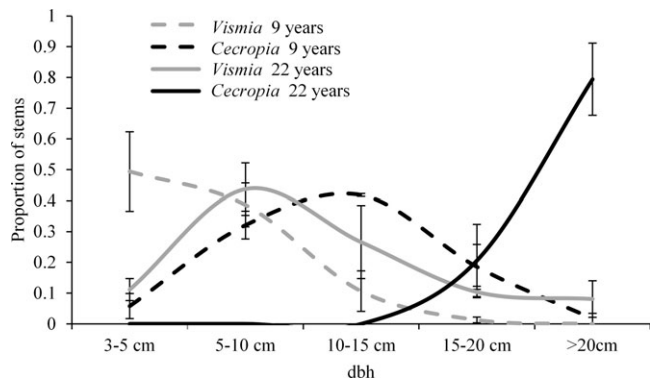


FIGURE 4. Size class distributions of stem diameters in secondary forests on abandoned pastures (*Vismia*) and abandoned clear-cuts (*Cecropia*) at 9 yr (dotted lines) and at 22 yr (solid lines). Multiple transects for 9-yr clear-cuts ($N = 2$), 22-yr clear-cuts ($N = 5$), 9-yr pastures ($N = 5$) and 22-yr pastures ($N = 3$) were used to find the average proportion of stems in five size classes (\pm SE). Curves were smoothed from the five size class data points.

occur if the C-P similarity increased through time until it was no longer significantly lower than either C-C or P-P similarities. Alternatively, both C-C and P-P could decrease until reaching the similarity level of C-P. Neither condition occurred during the time period of our study, in which we saw all three of these

similarities decrease, with P-P decreasing more rapidly than the other two. The decrease of P-P, C-C and C-P indicated that sites with the same history were diverging in composition but not becoming more similar to sites with different histories. This trend suggests that although the earliest pioneer assemblages were generally dominated by a small set of species characteristic of abandoned clear-cuts or abandoned pastures, through time secondary forest compositions became more varied, as in other tropical wet forest successions (Van Breugel *et al.* 2007, Dent *et al.* 2013). However, the diversity accumulation was sufficiently different in pastures and clear-cuts to preclude an increase in similarity between them (C-P). In prior research, abandoned clear-cuts were shown to increase in diversity substantially faster than in abandoned pastures (Williamson *et al.* 2014). If the composition of these two secondary forest types were eventually to converge, abandoned pastures would have to become as heterogeneous as clear-cuts, but prior review revealed divergence, not convergence, in species richness through time (Williamson *et al.* 2014). Divergence across sites as species richness increases during succession is typical of diverse communities like Amazon tree assemblages in contrast to less diverse ecosystems where succession exhibits convergence of sites on a climax assemblage (Walker *et al.* 2010).

Our analysis revealed differences in dominance along the alternative successional pathways. Both *Vismia* and *Cecropia*

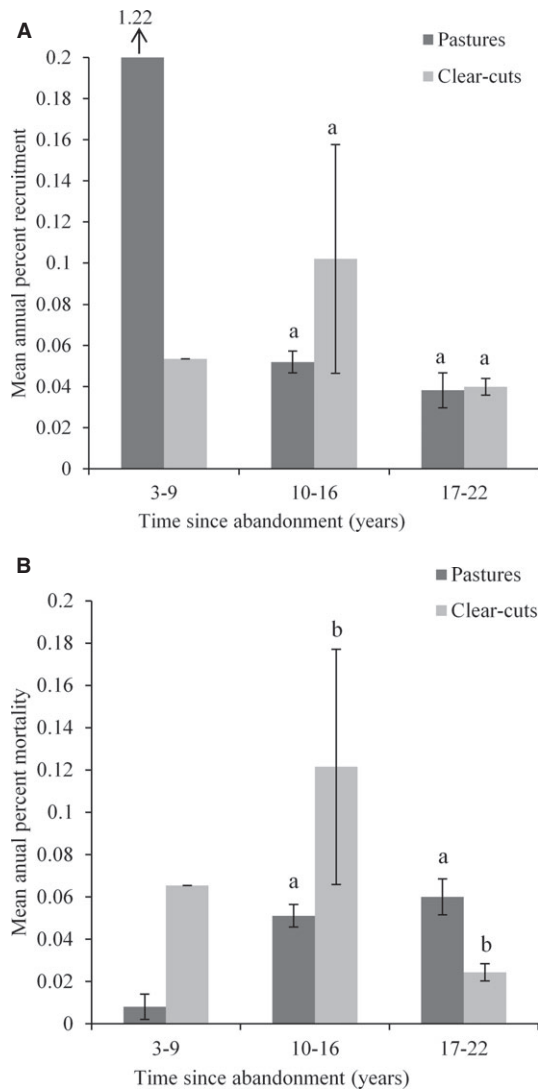


FIGURE 5. Turnover rates of all species of stems larger than 3 cm dbh in secondary forest transects of different land use histories and at different ages. (A) Average annual percentage recruitment (stems gained) for the periods 3–9, 10–16 and 17–22 yr after abandonment in abandoned pastures and abandoned clear-cuts. (B) Average annual percentage mortality (stems lost) during the same periods. Error bars are \pm SE and the numbers of transects are $N = 5$ (pastures 3–9), $N = 1$ (clear-cuts 3–9), $N = 8$ (pastures 10–16), $N = 2$ (clear-cuts 10–16), $N = 6$ (pastures 17–22) and $N = 7$ (clear-cuts 17–22). Statistical results for comparisons within age groups are shown.

dominance decreased with age in abandoned pastures and clear-cuts, respectively, but *Cecropia* declined more rapidly (Fig. 3). This result was consistent with more rapid species turnover evident previously in young abandoned clear-cuts (Norden *et al.* 2011). Higher dominance by *Vismia* was likely the result of greater initial dominance and greater life span. The size class distributions (Fig. 4) reflected the much slower growth of individuals and lower mortality of *Vismia* relative to *Cecropia*. For *Cecropia*, rapid growth and senescence may have caused the higher mortality in

clear-cuts during the first 16 yrs (Fig. 5). As saplings of mature forest species replaced *Cecropia* after 16 yr, the trend was reversed as mortality in clear-cuts decreased relative to pastures. Also, the higher stem mortality during the first 16 yr of succession likely contributed to greater turnover of species in clear-cuts. Thus, asymmetric competition and the subsequent thinning of dominants drive secondary succession and species turnover (Van Breugel *et al.* 2006).

Will *Vismia* transects eventually become more dissimilar in species composition? The paucity of new *Vismia* recruits in the oldest transects portends a declining population and subsequent replacement in plant succession. However, the current *Vismia* replacement in our older transects is consistently the same species, *Bellucia imperialis*, thereby maintaining the high P-P similarity values relative to C-C at 22 yrs. Therefore, compositional difference between clear-cuts and pastures are likely to persist at least until *Bellucia* loses dominance.

In secondary forests, smaller stems should forecast subsequent successional trajectories. In our 20-yr-old forests, none of the size classes showed convergence of abandoned pastures on abandoned clear-cuts or *vice versa*, supporting the conclusion that the difference in composition extended beyond the early dominants. However, smaller size classes were less similar to one another, with recruits in pastures as dissimilar as recruits in abandoned clear-cuts (Fig. 2A). Despite these decreases in similarity within treatments, the recruits were still more dissimilar between treatments than within them (Fig. 2A). Apparently, following the initially dominant pioneers, new species contribute to assemblage differences based on land use history, perhaps through niche specialization or dispersal. The initial difference in canopy dominants could produce niche differences in light and water availability in the understory or differences in seed rain from attraction of different dispersal agents. Recently Jakovac *et al.* (2012) did find differences in light transmitted through *Vismia* and *Cecropia* canopies as a function of stand age. However, Wieland *et al.* (2011) found that seed rain in both abandoned clear-cuts and pastures was limited to secondary species already present. Therefore, seed enrichment early in succession might offer a restoration practice to alter the trajectory of the pasture succession, perhaps even shifting it to the clear-cut successional pathway.

The two pathways may remain distinct indefinitely if there are underlying abiotic differences such as soil properties or climate. Although elsewhere cattle pastures are known to engender changes in soil properties, particularly through nutrient losses, a decline in organic matter and increase in soil compaction (Abril & Bucher 1999, Pereira *et al.* 2003, Álvarez-Yépez *et al.* 2008), extensive efforts to find soil differences underlying the *Cecropia* and *Vismia*-dominated successions have been largely unsuccessful. Gomes and Luizão (2012) tested for a dozen common soil properties and found only one difference, the C:N ratio in abandoned pastures was about 10 percent higher than in abandoned clear-cuts. They also found only one difference in 36 tests for cation differences, a case where one of three samples of Mg under *Bellucia* trees was 19 percent higher in pasture soils than in

non-pasture soils. Cation differences related to past prescribed burning and land use history occasionally appear in other Amazonian studies but inconsistently across studies (Uhl 1987, Buschbacher *et al.* 1988, Feldpausch *et al.* 2004, 2007, Gomes & Luizão 2012). Declines in N with prescribed burning have been documented in the eastern and central Amazon, but the differences were minor relative to differences in vegetation composition and biomass (Buschbacher *et al.* 1988, Feldpausch *et al.* 2007). In two studies, soil N was low, immediately following pasture abandonment, but often not lower than in the primary forest and it then accumulated quickly in the early yrs (0–14) of succession (Uhl 1987, Feldpausch *et al.* 2004). Overall, these studies do not present a strong case for soil properties explaining the vegetation differences between the alternative successional pathways derived from pastures and clear-cuts.

The potential of anthropogenic activities to generate novel communities has recently been highlighted (Lugo 2012). *Vismia*-dominated secondary forests fit the category of a human-induced, transient, species assemblage. Prescribed burning and grazing produce this alternative community by reducing the seed bank and advance regeneration, while favoring *Vismia*, a genera that is pre-adapted to fire relative to other species. Grazing may have a similar effect on regeneration as fire, however, the relative impact of these two factors in the area is not known. Not only do abandoned pastures differ in species composition from abandoned clear-cuts, but they also have a higher stem density, lower basal area, lower tree diversity (Williamson *et al.* 2014) and lower species turnover (Norden *et al.* 2011) than secondary forests growing in abandoned clear-cuts.

Our results provide evidence for persistence of alternative secondary successional pathways in the central Amazon—the initial floristic differences are maintained in some degree through several decades. Apparently, prescribed burning and grazing of pastures has fostered a new pathway that has yet to converge onto a more rapid pathway of forest succession. Thus, the abandonment of prescribed burning leaves a legacy that is not readily extinguished.

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SUPPORTING INFORMATION

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

APPENDIX S1. Results of statistical tests comparing C-C, P-P and C-P similarities for three size classes.

FIGURE S1. Map of the abandoned clear-cut transects and abandoned pasture transects at the BDFFP reserves, north of Manaus, Brazil.

FIGURE S2. Non-metric dimensional scaling plots for trees ≥ 3 cm dbh in abandoned clear-cuts and abandoned pastures.

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