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Research Article

Seed rain and advance regeneration in secondary succession in the Brazilian Amazon

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Abstract

Succession in the Brazilian Amazon depends on prior land-use history. Abandoned clearcuts become dominated by *Cecropia* trees and exhibit species replacements characteristic of natural succession in forest lightgaps. In contrast, abandoned pastures are dominated by *Vismia* trees that inhibit natural succession for a decade or more. Here we explore how advance regeneration and limited seed dispersal may contribute to the arrested succession in *Vismia*-dominated stands. Vegetation surveys showed that every *Vismia* stem in 3-8 year old *Vismia* stands originated as a re-sprout. In *Cecropia* stands, all tree species, including *Vismia,* originated mostly from seeds, after deforestation and abandonment. The 100% re-sprouts of *Vismia* in the abandoned pastures confirms that *Vismia* dominance results from re-sprouting following pasture fires. Seed rain in both *Vismia* and *Cecropia* dominated stands was limited almost exclusively to second growth species already reproducing in those stands, suggesting that the bats and birds foraging there were not bringing mature forest seeds into the second growth, but simply feeding and depositing local second growth species. As dispersal was similar in both stand types, dispersal differences cannot account for the ongoing dominance of *Vismia* relative to the ongoing successional transitions in *Cecropia* stands. Overall, advance regeneration in the form of *Vismia* re-sprouts is much more likely to be the driver of *Vismia* dominated succession than differential dispersal of mature forest seeds. In order to avoid extensive forest conversion into unproductive *Vismia* wastelands in the Amazon Basin, forestry permits for harvesting timber should include restrictions on subsequent anthropogenic degradation, such as conversion to pasture and prescribed burning.

Keywords: *Vismia*, *Cecropia*, secondary succession, seed dispersal, advance regeneration, Brazil, Amazon

Resumo

A regeneração florestal em áreas abandonadas na Amazônia depende, em primeiro lugar, na história de uso da terra. Áreas derrubadas seguidos de abandono são dominada por árvores de *Cecropia* e substituições apresentam espécies características de sucessão natural em clareiras. Em contraste, pastagens abandonadas são dominadas por árvores de *Vismia* que inibem a sucessão natural por uma década ou mais. Este estudo explora como a regeneração antecedência e a dispersão de sementes limitada, pode contribuir para a sucessão presada nas parcelas de *Vismia*. Levantamentos de vegetação mostraram que todos os troncos de *Vismia* nas parcelas de 3-8 anos de idade originaram-se como re-broto. Nas parcelas de *Cecropia*, todas as espécies, incluindo *Vismia*, originaram principalmente de sementes, após o desmatamento e abandono. Os 100% re-brotos de *Vismia* nas pastagens abandonadas confirma que a dominância de *Vismia* é o resultado de incêndios de pastagens. A chuva de sementes em ambos parcelas de *Vismia* e *Cecropia* era limitada quase exclusivamente às espécies da floresta secundária já reproduzindo nas parcelas, o que sugere que os morcegos e aves forrageando não traziam sementes da floresta madura para floresta secundária, mas simplesmente se alimentou e depositou espécies locais. Como a dispersão foi similar em ambos os tipos de dominância, as diferenças de dispersão não pode explicar a dominância de *Vismia* relativos às transições sucessionais em *Cecropia*. Em general, a regeneração avançada na forma de re-brotos é muito mais provável o condutor de dominância de *Vismia* que à dispersão de sementes florestais. A fim de evitar a conversão a florestas de *Vismia,* que são desertos improdutivos extensas na Bacia Amazônica, autorizações florestais para extração de madeira deve incluir restrições à degradação antrópica, tais como a conversão de pastagens e queimadas.

Palavras chave: *Vismia*, *Cecropia*, succesão secundária, dispersão de sementes, regeneração florestal, Brasil, Amazônia

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Introduction

In anthropogenically disturbed landscapes in the Neotropics, forest succession may be retarded due to competitive dominance by initial colonizers [1-5] or to limited dispersal of mature forest seeds [6, 7]. In the Brazilian Amazon, arrested succession on abandoned pastures is associated with numeric dominance by the genus *Vismia* [8]. In contrast, abandoned clearcuts are characterized by *Cecropia* along with a rich mix of other arboreal genera that exhibit species transitions characteristic of forest succession [8].

Vismia's initial abundance is a result of pasture fires prior to abandonment. *Vismia* can differentiate shoots from root tissue after stem loss, whereas *Cecropia* and other genera rarely survive repeated burns [9]. However, these monogeneric *Vismia* stands are often maintained for several decades, although the mechanism of ongoing dominance is not known [10]. In fact, it is not known whether the same initial re-sprouted *Vismia* trees last for several decades or whether *Vismia* replaces itself through several generations. In addition, *Vismia* may inhibit establishment of other mature forest species. In French Guiana, soil conditions and a well-shaded habitat, which assist in the growth of primary forest species, are found under *Cecropia* canopies but not under *Vismia* canopies [11]. In the upper Rio Negro basin, the regeneration of primary forest species is restricted under *Vismia* crowns, perhaps due to a change in soil conditions caused by the leaf litter [12, 13].

Alternatively, seed rain by mature forest species may be limited in *Vismia* stands due to a lack of avian dispersers. *Vismia* fruits are consumed mainly by bats, which may only bring a chiropterochore subset of forest seeds into *Vismia* second growth [14]. In contrast, most *Cecropia* species attract a broad set of disperser agents, such as birds, bats and primates, which may carry a more diverse array of mature forest seeds into *Cecropia* stands. Although *Vismia* stands are impoverished relative to *Cecropia* stands, species richness of both stand types declines with distance from primary forest, so seed dispersal may be limiting [8].

Here, we explore how aspects of two mechanisms--advance regeneration via re-sprouting and limited seed dispersal--may contribute to *Vismia* dominance of secondary forest on abandoned pastures in central Amazonia. Specifically, we determined the proportion of stems originating as re-sprouts for *Vismia* versus other genera in *Vismia*-dominated and *Cecropia*-dominated stands 3-15 years after abandonment. If re-sprouting ability is important beyond the first few years after pastures are abandoned, then a high proportion of *Vismia* stems originating from re-sprouts should still be evident in the older stands surveyed here. Second, in order to determine seed dispersal differences by bats and birds, we monitored the quantity and diversity of seeds that were dispersed into *Vismia*-dominated and *Cecropia*-dominated stands. Seed rain into *Vismia* stands may be depauperate compared to dispersal into *Cecropia* stands if bird-dispersed species are absent from *Vismia* stands.

Methods

Study Stands

The study area, located 80 km north of Manaus in the state of Amazonas, Brazil (2º 29’ S, 59º 41’ W, 54 m – 132 m elevation), is roughly 6 km east of the Biological Dynamics of Forest Fragments Project (BDFFP), a research collaboration operated by the Smithsonian Tropical Research Institute (STRI) and Brazil 's National Institute for Amazonian Research (INPA). The region is dominated by evergreen *terra firme* forest, and data collected at the BDFFP show a mean annual temperature of 26º C [15]. The climate is type Am in the Köppen [16] system: tropical humid with excessive rain in some months and an occasional month of less than 100 mm precipitation. The average annual rainfall recorded at the BDFFP is between 2,200 and 2,700 mm [17] with a dry season from June to October. The predominant soils are nutrient poor, clay-rich oxisols with yellow latosols and red-yellow podzols [18].

Study stands were established in young secondary forests on private lands along Zona Franca 7 (ZF7), a two-lane unpaved road northeast of the small town of Rio Preto da Eva, Amazonas state (Fig. 1). The lots on ZF7 are small, 250 m frontage by 1,000 m deep, and are surrounded by extensive old growth forest (Fig. 1). In the past, landowners deforested portions of their land to plant cassava and fruit trees and to harvest wood for charcoal production.

Eight second growth stands between 3 and 15 years after abandonment with different land-use histories were selected on the basis of subjective dominance by *Vismia* or *Cecropia* (Table 1). Distances between stands were at least 2 km to ensure independence of species composition. In each stand, all woody stems ≥ 3 cm diameter at breast height (dbh) were recorded in a 10 m by 100 m transect.

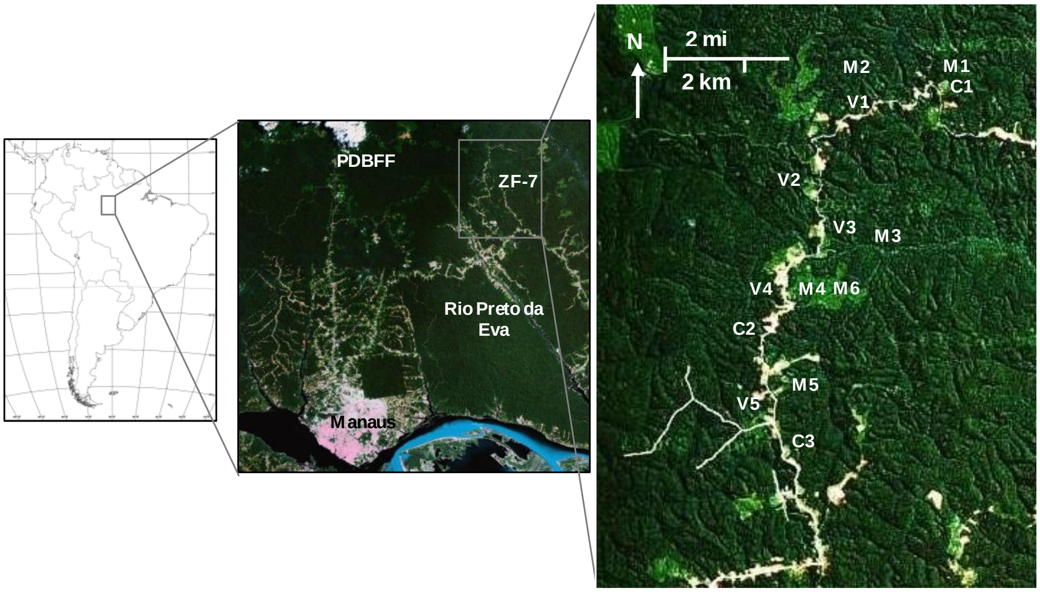

Fig. 1. Map of South America showing approximate location of the field site with inset of a satellite image of *Vismia* (V1-V5), *Cecropia* (C1-C3) and mature forest (M1-M6) stands

Re-sprouting

Inside the established 10 m by 100 m transects, we examined each woody stem ≥ 3 cm dbh to determine if it originated from seed or as a re-sprout. Stems were considered re-sprouts when they were visibly growing out of a remnant stump or when they shared remnants of other stems that had died. The latter condition indicated that there had been multiple re-sprouts, but that by the time of canopy closure usually only one stem had survived. The numbers and proportions of *Vismia*, *Cecropia*, and all other stems that originated as seedlings or as re-sprouts were tested for differences in stand type, *Cecropia* or *Vismia* (one factor ANOVAs with stands as replicates).

Table 1. Second growth stand characteristics and their land-use.

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Site Name	Dominant Genus	Years since Abandonment	Stand Size (m^2)	Land-use History
C1	*Cecropia*	8	10,000	Agriculture < 5 yrs
C2	*Cecropia*	4	7,500	Cleared & abandoned
C3	*Cecropia*	15	250,000	Cleared & abandoned
V1	*Vismia*	4	15,000	Orange grove
V2	*Vismia*	3	3,750	Cassava
V3	*Vismia*	8	1,875	Cassava, fruit trees
V4	*Vismia*	8	2,500	Cassava, guarana trees
V5	*Vismia*	3	4,000	Charcoal

Diurnal/Nocturnal Seed Traps

In order to monitor bird versus bat seed dispersal in *Cecropia* and *Vismia* stands, eleven 1- m^2 seed traps were spaced at 10 m intervals along each established 100-m transect. All traps were at least 10 m from the edge of the stand. Seed traps (Fig. 2) were constructed of 1-m tall PVC pipe frames which supported 1-mm nylon mesh suspended concavely to prevent seeds from bouncing or being washed out of the trap [19-22]. There were 55 traps in *Vismia* stands and 33 in *Cecropia* stands.

Fig. 2. Seeds were collected twice a day in seed-traps assembled in *Cecropia*-dominated second growth (shown) as well as in *Vismia*-dominated second growth

Seeds removed from traps at dawn (6:00 am) were assumed to have been dispersed by bats and those at dusk (6:00 pm) to have been dispersed by birds. To ensure that the seeds counted were those that had been handled by frugivores and not simply fruit fallen directly from the tree, only seeds with attached fecal matter were counted. Because it was impossible to be at all stands at 6:00 am or 6:00 pm on the same day, we sampled stands on a rotating basis for an average of seven days a month from June through August 2010.

Individual species seed abundances were $\log_{10}$ transformed and then tested for differences by stand type and by disperser type in 2-way ANOVAs with stands as replicates. In addition, we calculated species richness, Simpson's diversity index, and Shannon-Wiener diversity and evenness indices for seed collected from each stand. For bird-dispersed seeds, bat-dispersed seeds, as well as all seeds combined, we performed ANOVAs on the diversity metrics to determine differences between stand types. Finally, estimate S was used to determine separate individual-based species accumulation curves with 95% confidence intervals for all seeds collected in both *Vismia* stands and *Cecropia* stands [23].

Monthly Seed Traps

A second round of trapping was conducted monthly to compare seed rain by all dispersal modes in mature forest and in second growth stands. Seed traps, emptied monthly, not twice daily, were placed in the five second growth *Vismia* stands, the three second growth *Cecropia* stands, and also in six mature forest stands. Five mature forest stands were located within 100 m of adjacent *Vismia* second growth stands and the other mature forest stand was within 100 m of an adjacent *Cecropia* stand (Fig. 1). Eleven seed traps were established along 100-m transects within each of the six mature forest sites for a total of 66 traps in mature forest. In addition, the 11 seed traps per transect, used previously in the daily seed trapping, were opened monthly, in the five second growth *Vismia* stands and the three second growth *Cecropia* stands. Thus, overall there were 14 stands sampled monthly from January through May of 2010—six in mature forest, five in *Vismia* second growth and three in *Cecropia* second growth.

Monthly seed collections contained a mixture of seeds, fruits and litter. Due to limited time during the study, only half of the collections were sorted for analysis. In order to include data from all five months, January through May, seeds were sorted and measured from half the stands in January (14 days), February (28 days) and April (30 days), and the other stands in March (31 days) and May (31 days). All seeds, including those from fruits and feces, were dried, counted and identified to lowest practical taxon, usually to genus [24]. Uncommon seeds that could not be identified were grouped by morphotaxa. Also, the length of each seed was measured, and seeds were grouped into classes used by Cornejo and Janovec [24], whose book exhibits photos of many of the species' seeds. Size classes were: "Tiny": <0.5 cm at greatest length, "Small": 0.5-0.99 cm, "Medium": 1.0-1.99 cm, and "Large": >2.0 cm.

All seeds from all months in a stand were combined to calculate the number of seeds stand^{-1} month^{-1}. This variable was $\log_{10}$ transformed and tested for differences by stand type--*Cecropia*, *Vismia* and mature forest (ANOVA), for all seeds and for seed size classes separately. Where the ANOVAs indicated significant differences, treatments were compared pairwise by least squares means with Tukey's adjustment for multiple comparisons.

General Data Analysis

All ANOVAs were performed in PROC GLM of SAS 9.0 [25]. As seeds collected per trap were few, seeds were combined from daily or monthly collections and from multiple traps at each site, such that replicates were all the seeds collected at each stand; therefore, there was no provision for repeated measures in our analyses. The ANOVAS reflect differences across the eight stands for daily seed collections, and across the 14 stands for monthly seed collections. However, the values presented in tables and in the text are labeled to show seed numbers per sampling unit, such as seeds/trap/day or seeds/stand/month.

Results

Study Stands

Stands were originally characterized as *Cecropia* or *Vismia* dominated, based on our subjective assessment of vegetation (Fig. 3). Sørensen's modified index, based on species basal area, supported the classification of stands as *Vismia*-dominated and *Cecropia*-dominated. The pairwise similarities were not different between *Cecropia-Cecropia* (0.46 ± 0.06) and *Vismia-Vismia* (0.42 ± 0.08) comparisons (Mann-Whitney U=6.8, *P*=0.81), whereas *Cecropia-Vismia* (0.20 ± 0.11) similarities were significantly less than *Cecropia-Cecropia* (Mann-Whitney U=8.0, *P*=0.002) and *Vismia-Vismia* (Mann-Whitney U=8.5, *P*<0.0001) similarities.

Table 2. Density and basal area/transect, based on all stems ≥ 3 cm dbh, for five *Vismia* and three *Cecropia* second growth stands. "Non-VC" refers to non-*Vismia* and non-*Cecropia* stems. Abundances are per 0.10 ha transect. Relative abundance is calculated per transect.

	5 *Vismia* stands Mean ± SD	**3 *Cecropia* stands Mean ± SD**
Number of stands	5	3
Age of stands (years)	5.2 ± 2.6	9 ± 5.6
No. of trees ≥ 3 cm dbh	246 ± 20	248 ± 4
Basal area (m^2)	19 ± 2.7	30 ± 1.6
Species richness	36.4 ± 11.2	70.3 ± 9.5
Vismia abundance	127.0 ± 32.2	13.7 ± 5.9
Cecropia abundance	21.8 ± 21.0	48.3 ± 12.7
Non-VC abundance	97.2 ± 34.0	185.7 ± 20.8
Vismia relative abundance	0.52 ± 0.16	0.06 ± 0.02
Cecropia relative abundance	0.09 ± 0.08	0.20 ± 0.06
Non-VC relative abundance	0.39 ± 0.12	0.75 ± 0.07

Despite some difference in age of the stands, the mean number of stems was nearly identical in *Vismia*-dominated (246 ± 20; mean ± SD) and *Cecropia*-dominated (248 ± 4) stands ($F_{1,\ 6}$=0.02, *P*=0.89; Table 2). However, basal area (m) was greater in the *Cecropia* (30 ± 1.6) stands than in *Vismia* stands (19 ± 2.7; $F_{1,\ 6}$=36.71, *P*=0.009; Table 2). Both *Cecropia* and *Vismia* were much more common in their respective dominated stands than in the other genera's stands, for both absolute and relative abundances.

Species richness in *Cecropia* stands was double that in *Vismia* stands ($F_{1,\ 6}$=18.94, *P*=0.005; Table 2). The number and proportion of stems, not *Vismia*, nor *Cecropia* ("non-VC"), found in *Cecropia* stands were double the number and proportion in *Vismia* stands (total number: $F_{1,6}$=16.07, *P*=0.0070; proportion: $F_{1,6}$=22.41, *P*=0.0032; Table 2). In general, *Vismia* stands were heavily dominated by *Vismia*, whereas *Cecropia* stands exhibited much greater evenness among genera.

Re-sprouting

Every *Vismia* stem in *Vismia* stands was a re-sprout (N = 635). The proportion of *Vismia* stems that were re-sprouts in *Vismia* stands (1.00 ± 0.00, mean ± SD) was higher than in *Cecropia* stands (0.18 ± 0.12; $F_{1,6}$=286.16, *P*<0.0001), while the proportion of *Cecropia* stems that were re-sprouts in *Cecropia* (0.01 ± 0.01) and in *Vismia* (0.11 ± 0.21) were not different ($F_{1,6}$=0.67, *P*=0.44). For non-VC stems, the proportion of re-sprouts in *Cecropia* (0.22 ± 0.30) and in *Vismia (*0.24 ± 0.14) were not different ($F_{1,6}$=0.03, *P*=0.88).

The numbers of *Vismia*, *Cecropia* and non-VC stems that were re-sprouts in each stand type followed a pattern similar to the re-sprout proportions. The mean number of *Vismia* stems per stand that were re-sprouts in *Vismia* (127 ± 32) and in *Cecropia* (2 ± 1) were different ($F_{1,6}$=42.5, *P*=0.0006). The mean number of *Cecropia* stems per stand that were re-sprouts in *Cecropia* (0.33 ± 0.58) and in *Vismia* (2.2 ± 3.5) did not differ significantly ($F_{1, 6}$=0.79, *P*=0.41), and likewise, non-VC stems per stand that were re-sprouts in *Cecropia* (36.3 ± 47.9) and in *Vismia* (22.4 ± 10.8) did not differ significantly ($F_{1,6}$= 0.43, *P*=0.54).

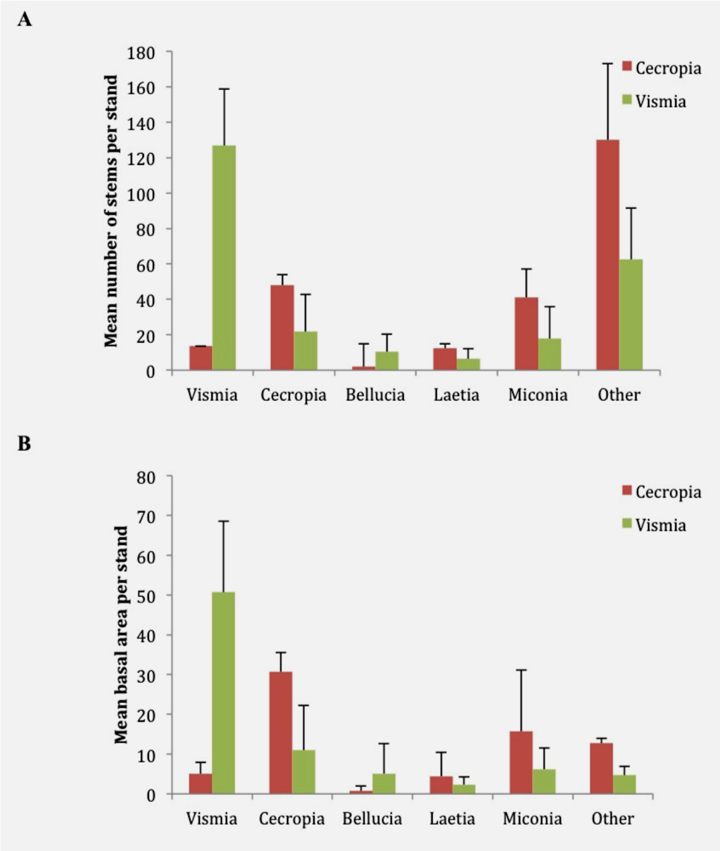

Fig. 3. Comparison of dominance (≥3 cm d.b.h.) of five most common second-growth genera based on mean density (A) and basal area (B) in *Cecropia* (N=3) and *Vismia* (N=5) dominated second growth stands (Mean ± SD). *Vismia* includes: *V. cayennensis, V. brasiliensis, V. guianensis, V. japurensis* and *V. sandwithii*; *Cecropia* includes: *C. concolor* and *C. sciadophylla*; *Bellucia* includes: *B. grossularioides* and *B. imperialis*; *Laetia* includes: *L. procera*; *Miconia* includes: *M. argyrophylla, M. burchellii, M. dispar, M. phanerostila, M. gratissima, M. lepidota, M. pyrifolia, M. regellii, M. tretraspermoides* and *M. tomentosa*.

Diurnal/Nocturnal Seed Traps

Seed traps were open in both *Cecropia* and *Vismia* stands for 169 nights and 154 days. Fecal samples collected in traps contained a total of 6,443 seeds. In *Vismia* stands, seed traps, open for a total of 102 days and 112 nights, collected 4,665 seeds, while traps in *Cecropia* stands, open for 52 days and 57 nights, collected 1,778 seeds. There was no significant difference ($F_{1,6}$=0.08 , *P*=0.79) in the number of fecal samples collected per trap-period (12hr) in *Vismia* (2.91 ± 1.21, mean ± SD, seeds/transect/trap-period) and in *Cecropia* stands (3.15 ± 1.15, seeds/transect/trap-period), and no difference ($F_{1,6}$=0.28, *P*=0.62) in seeds collected per trap period in *Vismia* (42.8 ± 39.8) and in *Cecropia* (29.4 ± 20.8) stands.

Seeds dispersed by birds were mainly in the genus *Miconia (*88.9%) regardless of second growth stand type (Fig. 4). Bat-dispersed seeds were predominantly in the genera *Vismia* (72.0%) and *Miconia* (15.6%) regardless of stand type (Fig. 4). Bats and birds deposited significantly different ($F_{1,12}$=8.53, *P*=0.013) numbers of *Vismia* seeds (0.019 per night and 0.00062 seeds per day). Bats and birds deposited significantly different ($F_{1,12}$=4.89, *P*=0.047) numbers of *Miconia* seeds (0.0027 per night and 0.0073 seeds per day). There were no significant differences in the number of *Cecropia* seeds or any non-VC seed species deposited by birds and bats in the two stand types, although numbers were generally too small to expect statistically significant differences.

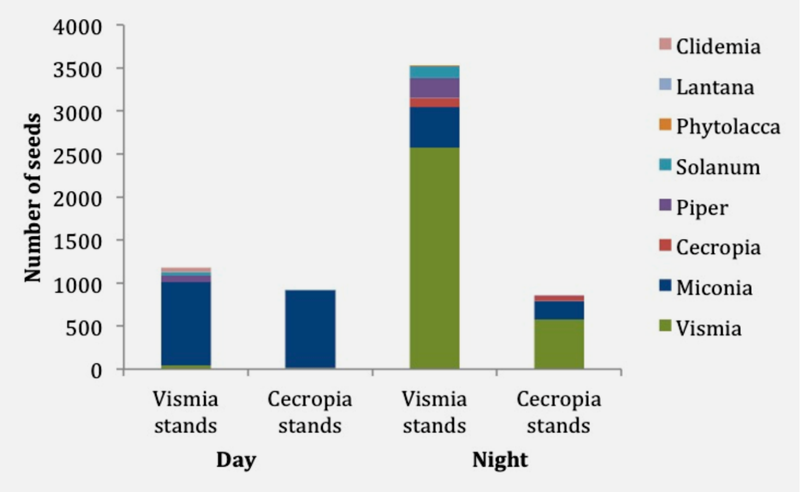

Fig. 4. Number of seeds collected in seed traps day and night in *Vismia* and *Cecropia* stands.

Vismia stands and *Cecropia* stands showed no significant difference ($F_{1,6}$=1.93, *P*=0.21) in species richness of seeds dispersed by birds (3.2 ± 1.5 and 1.7 ± 1.5, respectively) nor those dispersed by bats (3.0 ± 1.6 and 2.0 ± 0.0, per stand, respectively; $F_{1,6}$=1.12, *P*=0.33). There was a significant difference ($F_{1,6}$=6.70, *P*=0.04) in the species richness of all seeds dispersed in *Vismia* and in *Cecropia* stands (4.0 ± 1.0 and 2.3 ± 0.6, respectively) although this was a result of more individual seeds in *Vismia* stands. Species accumulation curves based on the number of individual seeds showed no significant difference in species richness between *Cecropia* and *Vismia* stands, as their 95% confidence intervals overlapped extensively. The number of species accumulated was only five in *Cecropia* stands and seven in *Vismia* stands, and the combined total was eight, with four species in common. For Simpson's diversity and Shannon-Wiener's diversity and evenness, there were no significant differences by stand type.

Monthly seed traps

More seeds were trapped per month in *Vismia* stands (13,926 seeds $month^{-1}$ $stand^{-1}$) than in *Cecropia* stands (304 seeds $month^{-1}$ $stand^{-1}$) or in mature forest (17 seeds $month^{-1}$ $stand^{-1}$). By species, significantly more *Vismia* seeds $month^{-1}$ $stand^{-1}$ were collected in *Vismia* stands than *Cecropia* stands (t_{10}=-6.71, Tukey adj. *P*=0.0001; Table 3), more *Cecropia* seeds $month^{-1}$ $stand^{-1}$ were collected in *Cecropia* stands (t_{10}=-0.79, Tukey adj. *P*=0.01), and more unknown seeds $month^{-1}$ $stand^{-1}$ collected in mature forest stands (t_{10}=-3.72, Tukey adj. *P*=0.01).

There were many, many tiny seeds and very few larger seeds, especially in the second growth stands (Table 3). In order to test for differences in sizes, the two classes “tiny and small” were combined into one class, “little”, and the two classes “medium and large” were combined into one class, “big”. There were significant differences in the number of little and big seeds collected: more big seeds month^{-1} stand^{-1} collected in mature forest than in *Vismia* stands (t_{10}=6.77, Tukey adj. P<0.0001; table 3) and more in mature forest than in *Cecropia* stands (t_{10}=-6.18, Tukey adj. P=0.0001). Conversely, there were more little seeds month^{-1} stand^{-1} collected in *Vismia* stands than in mature forest (t_{10}=-7.39, Tukey adj. P<0.0001); more in *Cecropia* stands than in mature forest (t_{10}=3.73, Tukey adj. P=0.004); and more in *Vismia* stands than *Cecropia* stands (t_{10}=-2.67, Tukey adj. P=0.023). Data were $\log_{10}$-transformed prior to testing.

The diversity of seeds (Shannon-Wiener Index, H), species richness (S) and evenness (E) of monthly seed collections for all stands of a type combined were highest in mature forest (H: 1.4; S: 30; E: 0.75) and lowest in *Vismia* stands (H: 0.08; S: 9; E: 0.29) with *Cecropia* intermediate between the two (H: 0.59; S: 7; E: 0.59).

Table 3. Abundance of *Vismia*, *Cecropia* and unknown seeds collected in *Cecropia* stands, *Vismia* stands, and mature forest, month^{-1} stand^{-1} (Mean ± SD), in the four original size classes (Tiny: <0.5 cm, Small: 0.5-0.99 cm, Medium: 1.0-1.99 cm, Large: >2.0 cm), and in the combined classes (Little: 0.01-0.99 cm and Big: ≥1.0 cm) for statistical tests.

Seed Type	***Vismia* stands**	***Cecropia* stands**	**Mature forest**
Vismia	29,873.80 ± 29,873.32	10.33 ± 17.04	0 ± 0
Cecropia	47.80 ± 78.92	586.00 ± 850.55	6.40 ± 14.31
Unknown	1.00 ± 1.00	2.33 ± 2.52	20.20 ± 17.37
Tiny	29,976 ± 29,850	636.33 ± 811.24	6.40 ± 14.31
Small	0.20 ± 0.45	1.33 ± 2.31	0 ± 0
Medium	0.40 ± 0.55	0.33 ± 0.58	17.80 ± 17.74
Large	0.40 ± 0.89	0 ± 0	2.60 ± 2.19
Little	29,977.00 ± 29,850.05	637.67 ± 810.34	6.40 ± 14.31
Big	0.80 ± 0.84	0.33 ± 0.57	20.40 ± 17.54

Discussion

Forest regeneration following anthropogenic disturbances such as clearcutting and conversion to agriculture or pasture often deviates from the pathway of secondary succession that follows natural perturbation of mature forest. Anthropogenic land use is believed to alter soil conditions [26, 27] and to affect initial florisitics through changes in the advance regeneration, the soil seed bank, and seed rain [28-32]. In such landscapes, succession may be retarded due to soil compaction, nutrient depletion, dispersal limitation of mature forest propagules [6, 7, 26, 29, 32, 33] or competitive dominance by the species initially present [1-5, 8, 28-31]. Lianas, commonly found during gap-phase regeneration, may take advantage of high light levels and relatively low canopy heights to impede secondary succession [3, 4]. Similarly, grasses, sometimes in association with fire, have been shown to delay succession [1, 2, 5]. Several of these factors may operate jointly--for example, a depleted seed bank, limited seed rain, and abundant seed predation--to restrict recruitment into secondary succession [32].

In a fragmented landscape that includes anthropogenic and natural elements, how succession will proceed often depends on prior land use history and proximity to mature forest. Throughout much of the Amazon Basin, abandoned pastures are often dominated by species of *Vismia* because it is the only tree genus capable of regenerating shoots from below ground tissues [8, 9, 34]. Repeated burning of pastures kills other advance regeneration and seedlings stimulated to germinate from the seed bank. Where recruitment limits succession, distance to mature forest becomes critical [8, 32].

Here, we explored questions related to two factors, advance regeneration and seed dispersal, in young *Vismia*-dominated stands, relative to natural succession in *Cecropia*-dominated stands [8]. First, how important was *Vismia* re-sprouting and was the initial abundance resulting from the re-sprouting still evident a decade after pasture abandonment? Second, was seed rain into *Vismia* stands different from seed rain into *Cecropia* stands and were there differences in bat and bird dispersed seeds associated with the two stand types?

Composition of the stands studied here reflected the land-use histories in a manner similar to that described by Mesquita et al. [8]; areas that were used for short-term agriculture or that were abandoned shortly after being cleared had a diverse species composition and were dominated by individuals in the genus *Cecropia*, whereas areas used for crops or for charcoal production, and thus repeatedly burned prior to abandonment, were dominated by *Vismia* (Fig. 5).

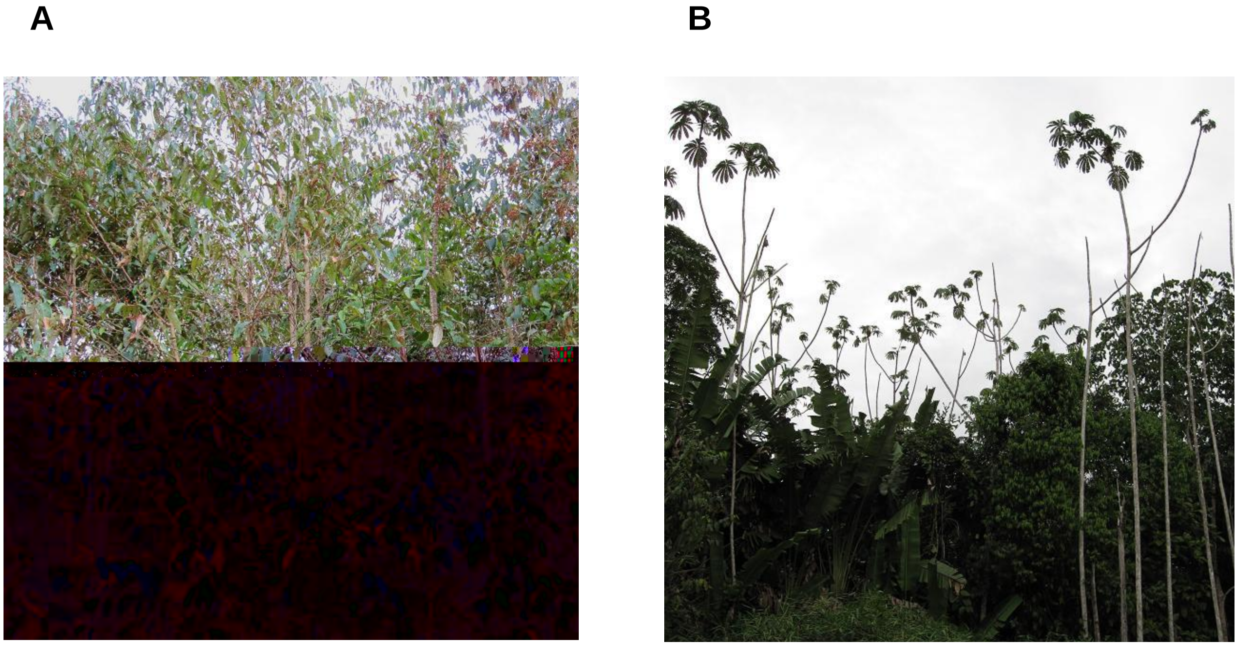

Fig. 5. Second growth stands in central Amazonia are dominated by either *Vismia* (A) or *Cecropia* (B)

Re-sprouting

In regard to the importance of re-sprouting, our results were unanimous: 100% of the *Vismia* stems in the 3-8 year old abandoned pastures were re-sprouts. Thus, pasture maintenance, which requires periodic burning, produces an initial composition of re-sprouts of *Vismia* that remain dominant for at least eight years after abandonment. Given that *Vismia* is known to maintain its dominance in abandoned pastures for at least two decades [8, 10], and here we have shown that the stems in 8-year old stands were all derived as re-sprouts, then it is reasonable to assume that the same re-sprouts will continue their dominance for one or two decades. *Vismia* trunks in 20-yr old abandoned pastures no longer have remnant stumps visible, but multiple-stemmed individuals attest to a re-sprouting origin [34].

In contrast, *Vismia* stems in *Cecropia* stands were overwhelmingly (82%) from seed, not from re-sprouts. *Vismia* is a component of natural regeneration in forest light gaps and clearcuts. In gaps the stems originate from seed, not re-sprouts [34]. Therefore, it is no surprise to find individuals derived from seed in unburned secondary forests. However, the number of *Vismia* individuals in *Cecropia* stands was only one-tenth the number in *Vismia* stands.

Vismia in the upper Rio Negro colonizes abandoned slash-and-burn parcels, but apparently as much from seed as from sprouts [35]. In contrast to abandoned pastures, dominance on such agricultural land wanes more quickly, within the first five years [36]. However, in the eastern Amazon, dominance by *Vismia* apparently varies with the intensity of land use, but lasts at least a decade following moderate to heavy land use [28].

In our study, *Cecropia* stems were nearly all from seed, 99% in *Cecropia* stands and 89% in *Vismia* stands, as expected because the two species here, *C. sciadophylla* and *C. concolor*, do not re-sprout when the main stem is killed by fire. A few *Cecropia* stems sometimes survive pasture fires, originating as re-sprouts where the basal stems of burned trees were protected from the flame front by rocks or fallen logs. Other *Cecropia* species in the Central Amazon are also killed by fires, although in Brazil's coastal rain forests *C. glazioui* re-sprouts from lateral roots after fire much like *Vismia* [9, 33].

Stems of species other than *Vismia* or *Cecropia* in our study were about 75% from seed in both stand types. Similar re-sprouting rates in the two stand types imply that the stems originated from seeds dispersed after land abandonment and are not related to fires. Re-sprouting at a 25% rate commonly results from partial stem damage by herbivores and falling litter. Despite equal rates of re-sprouts among the stems, these other species' stems were twice as abundant in *Cecropia* stands as in *Vismia* stands.

Seed Dispersal

The majority of seeds collected in seed traps were pioneer species commonly found as adults in the second growth in which the seeds were collected, indicating that dispersers were consuming and depositing seeds in second growth rather than moving between mature forest and second growth stands. Quantitative differences in seeds collected in the two stand types reflected the composition differences of adults in the stands -- most notably, more *Vismia* in *Vismia* stands. Outside of five unknown seeds, all the seed rain was from the same pioneer species present in the stands where the traps were located. Monthly seed rain did yield larger, unidentified (cf. mature forest) seeds in traps in the mature forest, but not in the secondary stands, so even though seeds were being produced in mature forest, they were not transported into the second growth stands. The same conclusion was reached in an earlier study comparing seed rain in a 6-year old *Vismia* stand and in nearby primary forest; over 14 months 96 seed morphotaxa were identified from traps in primary forest but only 9 morphotaxa from traps in the *Vismia* stand [37]. Thus, even though seed diversity is high in primary forest, seed dispersal into nearby second growth is low.

There were some differences in the day and night seed collections, reflecting dispersal by birds versus bats. In both stand types, birds dispersed mostly *Miconia* seeds and bats dispersed mostly *Vismia* seeds; however, seeds from both genera were found in fecal samples from both disperser types. Although birds and bats are known to specialize in different genera of seeds [38, 39], bats are more specialized in fruit selection, rarely sampling ornithochore fruits, whereas birds sometimes consume chiropterochore fruits [40-43]. However, neither group in our study dispersed a diverse array of seed species. This result suggests that fruit consumption in early secondary vegetation involves species whose activities are restricted to secondary vegetation, for both birds [44] and bats [45]. Capture rates of bats have been shown to be roughly equivalent in young *Vismia* and young *Cecropia* stands with the three most abundant species, *Carollia perspicillata, Rhinophylla pumilio*, and *C. brevicauda*, accounting for 90% of the captures [45]. The three species are small and unlikely to carry primary forest seeds.

We had expected that seeds dispersed in *Cecropia*-dominated stands would be more diverse than those in *Vismia*-dominated stands, on the assumption that *Cecropia* fruits would attract a more diverse set of dispersal agents [38-42], notably birds. This was not the case, at least for the months studied here. There were only five species of seeds dispersed in *Cecropia* and seven in *Vismia*--clearly unrepresentative of regeneration in nearby mature forest that contains over 1000 tree species [46]. Seed rain in both stand types was relatively species poor, and species accumulation curves confirmed no significant difference in seed species richness between stand types. Birds that foraged and deposited seeds in both stands were small and unlikely to disperse larger primary forest seeds. Birds large enough to consume large-seeded fruits are generally uncommon in human-modified landscapes [47]. In our stands, toucans and guans were never seen.

Where, then, are the seeds of the 1000+ tree species that occupy nearby, old growth forests? One might argue that our seed trap sampling, performed only during June to August, missed the fruiting season of many tree species. The incidence of fruiting is highly variable among primary forest species in the Central Amazon north of Manaus [48-53]. Among pioneers, the highest number of species fruit from January to March, although many species fruit continuously throughout the year [53]. Neither our monthly seed collections from January to May nor our daily collections in June, July and August demonstrated seed rain from nearby mature forest into adjacent second growth stands. Therefore, the most reasonable explanation is that dispersal agents are not moving seeds from mature forest into the second growth stands. Apparently, the birds and bats visiting second growth are mostly restricted to second growth, and more specialized dispersers such as primates, terrestrial mammals, as well as larger birds and bats that inhabit mature forest, are rare visitors to early secondary vegetation. Second-growth birds and bats may well be a distinct group from the primary forest species [44, 45].

Conclusions

In the Central Amazon, the slow turnover rate in *Vismia* second growth stands, originating in abandoned pastures, is an exemplary case of arrested succession [8-10]. Mesquita et al. (2001) showed that as distance from primary forest increases, species richness declines, suggesting that seed dispersal limits plant recruitment to some degree in young second growth. Our results support limited dispersal of seeds of mature forest species into second growth. Seed rain in both *Vismia* and *Cecropia* stands overwhelmingly reflected the dominant secondary species fruiting within each stand type. But neither birds nor bats brought new species into the second growth stands. Therefore, differences in rates of succession in *Vismia* and *Cecropia* stands are probably not a result of differences in seed dispersal by the bird and bat species visiting these young secondary forests. Consequently, some other process is operating to determine the alternative successional pathways.

Vismia stems in *Vismia* stands were 100% re-sprouts, demonstrating that they originated from stems burned in pasture fires. Their continued dominance for several decades may result simply from longevity and perhaps as well from inhibition of other species seedlings, although our seed rain data indicate that few mature forest seeds are dispersed into second growth stands. Without input of mature forest seeds, numeric dominance by the initial flora continues to provide dominance by default.

Overall, it appears that the alternative successional trajectories that characterize abandoned clearcuts versus abandoned pastures [8, 10] are a result of initial species composition which results in species replacements in the *Cecropia* stands and few replacements in *Vismia* stands. For the first decade or two of secondary succession, *Vismia* appears to maintain its dominance. This pattern of diverted or arrested succession on abandoned pastures is widespread, but not universal. *Vismia* dominance characterizes the ancient and nutrient poor soils of the Central and Eastern Amazon Basin, defined geomorphologically by the Guiana Shield and the Brazilian Highlands. Likewise, the soils of the Atlantic coastal forests are extremely old. However, in the Western Amazon and much of Central America, where soils are richer and geomorphologically younger, patterns of succession are different from those in the Central Amazon, and arrested successions by *Vismia* are uncommon. Therefore, *Vismia* dominance of abandoned pastures though re-sprouting after fires may be limited to ancient soils that are nutrient poor [54].

Implications for Conservation

High intensity land-use has been linked to *Vismia*-dominated successional forests in Brazil [1, 9, 43, 55], French Guiana [11], and Colombia [36]. Secondary succession on these abandoned lands depends on land use history, dispersal from the nearest seed sources [8] and the ability of forest species to re-sprout. Succession in abandoned pastures is arrested because the *Vismia* re-sprouts maintain dominance for at least one or two decades. Seed dispersal of mature forest species into *Vismia*-dominated stands is close to nil, but this is no different from dispersal into *Cecropia*-dominated stands where succession is not arrested. Therefore, the arresting mechanism lies in the early years following abandonment when *Vismia,* surviving pasture burns, becomes dominant by default.

The elimination of other woody species results from repeated prescribed fires, usually with anthropogenic intent of reducing woody regeneration to the benefit of forage grasses. Repeated burning reduces seed and seedling banks and kills remnant re-sprouts of mature forest species. Meanwhile, re-sprouting by the pioneer genus *Vismia* is prolific, resulting in monogeneric second growth within which other species are extremely slow to recruit. By contrast, in *Cecropia* stands, a diverse seed bank, seedling bank and remnant forest re-sprouts produce an enriched flora that regenerates under maturing *Cecropia* trees.

In order to avoid depauperate wastelands dominated by *Vismia*, we recommend that clear cutting of primary or older secondary forests should be accompanied by a post deforestation program that effectively limits or taxes land that is burned and converted to pasture. Deforestations occur first and foremost for timber, but deforestation is often followed by less lucrative charcoaling of stumps and slash, and conversion to cattle pastures. Forest conversion to pasture is a form of “pasteurization” of the regeneration resources. As most of the forest value lies in the timber extracted, clearcuts should be abandoned without conversion to pasture.

Enrichment plantings in abandoned pastures have been recommended for some tropical secondary forests in the tropics [56], but studies suggest otherwise in *Vismia* stands. Experimental transplants have exhibited extremely slow growth short term, suggesting that young *Vismia* stands inhibit mature forest seedlings [57 and

Jakovac pers. com.], although long term studies are needed. Enrichment with seeds of pioneers or mature forest species has had limited success [58] although growth improves when *Vismia* is removed [59]. Abandoned pastures in the Amazon Basin are overwhelmed by *Vismia* re-sprouts, so enrichments that function in tropical grasslands [55, 60-62] may prove unsuccessful in *Vismia* stands. Likewise, attempts to attract dispersal agents with roosts [63] or tree islands [64, 65] hold little promise where *Vismia* has already assumed dominance. Planting saplings in artificial gaps may be more successful, but at greater effort and expense.

Clear cutting of *Vismia* stems is time and cost intensive. As traditional, ecological restoration schemes offer little hope of regenerating old growth Amazonian forests, effective control mechanisms for *Vismia* stems need to be developed. Given the extensive monogeneric stands now available, finding uses for *Vismia* stems could result in harvests that might facilitate reversion to natural succession. Otherwise, natural regeneration in abandoned pastures will have to wait for senescence of a generation of *Vismia* trees.

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