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Contrasting community compensatory trends in alternative successional pathways in central Amazonia

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Based on eight years of annual censuses in secondary forests in central Amazonia, we compared successional dynamics in areas presenting alternative states due to different land use histories. Sites that had been clearcut without subsequent use are dominated by the pioneer genus *Cecropia*, but their understory is characterized by a diverse species assemblage. In contrast, areas clearcut and then used for pasture are dominated by the genus *Vismia,* forming nearly monogeneric stands. We evaluated whether such patterns were the outcome of differences in community compensatory trends, leading to a dynamic system of sequential replacement of species in *Cecropia* stands, and to a persistent stage of succession in *Vismia* stands. Floristic turnover in *Cecropia* stands showed strong and consistent negative frequency dependence. In contrast, *Vismia* stands exhibited little or no frequency dependence, likely due to local competitive interactions or priority effects. In these stands, species of the genera *Vismia* and *Bellucia* remained dominant throughout the monitoring period, whereas species initially of low abundance and frequency remained so. Differences in recruitment were the major driver of these alternative states. As species colonization proceeds, we expect dominance in the *Vismia* stands to diminish, albeit slowly. Our approach proved to be a useful tool for comparing species turnover in systems presenting alternative states.

Unraveling the mechanisms driving patterns of plant community reassembly after disturbance remains a major challenge to an integrated understanding of successional dynamics in species-rich communities (Finegan 1996, Chazdon et al. 2007, van Breugel et al. 2007, Chazdon 2008a). Models of secondary succession typically rely on deterministic processes, in which changes in species abundance over time are mainly predicted by life history attributes (Finegan 1996, Rees et al. 2001, Chazdon 2008a). Under this scenario, the community will slowly reach an equilibrium state, potentially recovering from the past perturbation (Finegan 1996). Although many reassembling communities follow this model (Young et al. 2001, Chazdon 2003), it has been increasingly recognized that degraded systems may develop toward alternative, persistent states (sensu Suding et al. 2004), exhibiting low resilience to their original condition. Such divergence in successional pathways may be caused by dispersal limitation, by differences in abiotic factors, or by priority effects resulting from competitive advantages of initial colonizers (Young et al. 2001). This pattern was described as the "inhibition model" by Connell and Slayter (1977), and has been reported in many types of communities, including temperate prairies (Anderson et al. 2000), chaparral (Halligan 1975, Muller et al. 1964), lake systems (Boerner 1985), coral reefs (Nystrom et al. 2000), and tropical rainforests (Mesquita et al. 2001, Schnitzer and Bongers 2001, Hooper et al. 2004). Despite this wide documentation, a broad conceptual framework addressing the mechanisms driving such alternative states in degraded landscapes is lacking (Suding et al. 2004).

The sequential species replacement typically observed in successional communities is the result of important shifts in species relative abundance over time, where the initially abundant pioneer species experience higher rates of mortality, and the locally rare, shade-tolerant species are favored (Finegan 1996). Such temporal interchange in species dominance is driven by differences in lifespan and growth rates among early- and late-successional species (Gomez-Pompa and Vazquez-Yanez 1981, Finegan 1984). The outcome of this pattern, however, corresponds to that of negative frequency dependence where rare species have an advantage over abundant ones (Janzen 1970, Connell 1971). If co-occurring species share similar responses to population abundance, a community compensatory trend (CCT) will emerge during succession - that is, a negative relationship between species population growth rates and relative abundance (Connell et al. 1984, Chesson 2000, Adler 2007). In secondary successions exhibiting persistent alternative states, however, a CCT does not seem to occur. Instead, the monodominance by a particular species suggests that positive feedbacks might be reinforcing the persistent state, altering ecological resilience (Suding et al. 2004). These patterns will coincide with the outcome of communities exhibiting positive frequency dependence, or lacking negative frequency dependence.

Demonstration of a CCT requires that less frequent species exhibit increased performance compared to frequent species. This process implies that population performance changes over time with changes in species relative abundance, leading floristic composition to fluctuate, as in dynamic systems (Webb and Peart 1999, Wright 2002). Although changes in species frequency over succession are the result of interspecific rather than intraspecific interactions, a CCT provides a valuable framework to quantitatively assess shifts in species relative frequency in plant communities undergoing floristic reassembly. Such conceptual models that incorporate vegetation dynamics are a critical element for the development of predictive tools guiding restoration and management efforts (Suding et al. 2004).

Mesquita et al. (2001) reported the occurrence of two distinct successional trajectories in central Amazonia, north of Manaus, where patterns of species richness and composition depend upon land-use history. Forests that were clearcut with no subsequent land use are dominated by species in the pioneer genus *Cecropia*, and their understory is characterized by a diverse species assemblage. In contrast, abandoned pastures, which were burned yearly, are dominated by species in the pioneer, fire-induced resprouter genus *Vismia*. These forests form nearly monogeneric stands, with poor representation of mature forest species in the seedling layer (Mesquita et al. 2001, Williamson and Mesquita 2001), and appear to maintain high frequencies of small stems, indicative of self-replacement (Mesquita et al. 2001). However, Mesquita et al. (2001) study is based on static data, and it is not clear to which extent these two alternative pathways tend to converge later in succession. Indeed, several stands in the region are mixed forests that do not show any sign of the identity of the initial dominants (Mesquita unpubl.).

Here, we used eight years of vegetation dynamics data from secondary forests in the same study area as Mesquita et al. (2001) to develop a novel approach for assessing successional dynamics in secondary forests. We evaluated shifts in species relative abundance, and modeled frequency dependence in order to quantify rates of vegetation change and infer successional pathways in both types of forest. If *Vismia* stands are destined to become monodominant forests, then we expect them to show lack of CCT resulting from either a positive or no frequency dependence (Fig. 1a–b). If, in contrast, their successional pathway is slowly converging towards that of *Cecropia* stands, these stands should manifest a CCT, resulting from negative frequency dependence (Fig. 1c–e). To test these predictions, we first evaluated changes in dominance over time in both *Cecropia* and *Vismia* stands. Then, we used maximum likelihood techniques to estimate the strength and the direction of frequency dependence in these two types of forest. We evaluated the effect of frequency dependence in changes in species relative abundance over succession at both the recruitment and survival level, as these two processes may affect population growth separately.

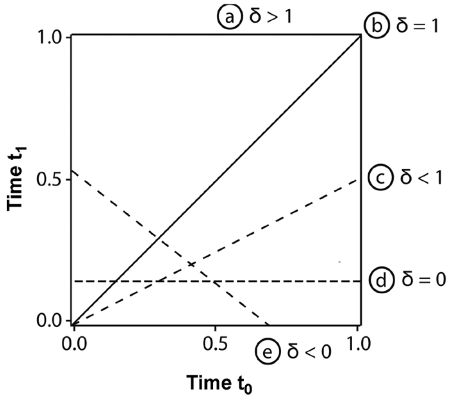

Figure 1. Conceptual framework of the possible scenarios of frequency dependence. (1) positive frequency dependence: the most frequent species show a higher per capita growth rate relative to the others, leading to monodominance, (2) no frequency dependence: species frequency does not change over time, the relationship is monotonic, (3) negative frequency dependence: the more frequent species are reduced in frequency over time, leading to a more even pattern in species frequency distribution, (4) null model: species frequency at time 1 is unrelated to species frequency at time 0, (5) strong negative dependence: species frequency shifts so that frequent species become rare species and vice versa.

Material and methods

Study sites

This study was conducted about 80 km north of Manaus, in the state of Amazonas, Brazil, in the same region where the Biological Dynamics of Forests Fragments Project (BDFFP) investigates the effects of forest fragmentation (Bierregaard et al. 2001). Average annual rainfall is ca 2600 mm with a mild dry season between July and November. 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 study sites were clearcut of mature forest at the beginning of the 1980s. Much of this area was converted to pastures and burned repeatedly for several years before abandonment. The forest that regenerates following this land use is typically dominated by species of the genus *Vismia,* which apparently are the only tree species capable of regenerating after multiple burns. Clearcuts that were abandoned with little or no burning are dominated by species of the genus *Cecropia*, which are characterized by high growth rates and short life spans.

Eighteen transects were established in 1999 in second growth vegetation, and ten were further established in 2000 and 2002. Among these 28 transects, monitoring was discontinued in ten that were cleared a second time. This study is based on the 19 transects that have at least six years of long-term data. These transects are located within three farms, Porto Alegre, Dimona and Esteio (Table 1, Fig. 2). Following clearcutting in the early 1980s, the three farms had different histories, producing different mosaics of secondary vegetation. Of the three farms, only Porto Alegre was never burned. However, several of the fires to keep the

Table 1. Table summarizing the characteristics of the 19 study transects.

	Vismia					*Cecropia*				
Farm	Transect	Age (years)	Year of 1st census	Times burnt	Sampling area (m^2)	Transect	Age (years)	Year of 1st census	Times burnt	Sampling area (m^2)
Esteio	Colosso-1	11	1999	3	500	Florestal-6	16	1999	0	300
	Cabo frio-3	11	1999	2	200	Florestal-7	16	1999	0	300
	Cabo frio-4	11	1999	2	200	C.Powell-22	19	2002	0	300
	Florestal-5	9	1999	4	500	C.Powell-23	19	2002	0	300
Dimona	Dimona-14	5	1999	7	100	Dimona-17	17	1999	0	300
	Dimona-15	9	1999	4	250	–	–	–	–	–
	Dimona-16	7	1999	5	100	–	–	–	–	–
Porto Alegre	–	–	–	–	–	P.Alegre-12	16	1999	0	300
	–	–	–	–	–	P.Alegre-13	16	1999	0	300
	–	–	–	–	–	P.Alegre-21	5	2000	2	600
South Esteio	Diva-8	9	1999	2	500	–	–	–	–	–
	Diva-9	8	1999	4	500	–	–	–	–	–
	Km 21-10	2	1999	2	600	–	–	–	–	–
	Km 17-11	8	1999	6	250	–	–	–	–	–

fragments of the BDFFP isolated have spread into adjacent second growth, with the result that *Vismia* established successfully in these areas. Both Dimona and Esteio farms were converted into pastures after the initial clearcut, and were maintained as such for 5–8 years before being abandoned. *Cecropia* transects at Dimona and Esteio are located at the extreme edges of the ranches where fires rarely penetrated. Eight transects are located in Esteio, four in Dimona, and three in Porto Alegre (Table 1). The four remaining transects are located between the ranches. Three of these are abandoned rubber plantations, which were clearcut, planted in *Hevea brasiliensis*, and abandoned. These plantations were subject to prescribed burning, so the secondary growth is dominated by *Vismia*. The fourth transect is abandoned manioc that has converted to *Vismia* regeneration.

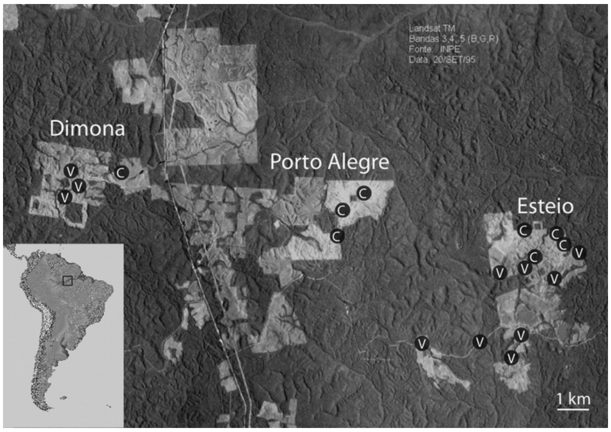

Figure 2. The study area within the Biological Dynamics Forest Fragment Project showing the location of the eleven *Vismia* (V) and the eight *Cecropia* (C) transects within each of the three farms: Dimona, Esteio and Porto Alegre. The image was acquired by the Landsat TM satellite sensor on September 20, 1995 (bands 3, 4, 5 viewed here in grayscale). Mature forests around the three farms appear dark gray whereas lighter shades on the farms are successional forests and managed pastures. The inset image shows the location of the study area in the Amazon Basin.

Tree census transects

Transects of different ages since abandonment were selected to obtain a chronosequence. Transect age at the initial census varied between two and 19 years after land abandonment. Because *Cecropia* transects were abandoned earlier, transects dominated by *Vismia* are typically younger. Previous analyses showed that such differences in age since abandonment did not bias the observed patterns (Mesquita et al. 2001). The area of each transect varied between 100 m^2 to 600 m^2 (Table 1). Widths were greater for older transects that contained fewer stems. In each transect, all woody stems $>$ 3 cm DBH were inventoried. During annual censuses, recruits into the 3-cm DBH were inventoried, and stems were recorded as dead if no living tissues could be observed. For multiple-stemmed individuals, only the largest stem was considered. Stems of *Vismia* species that were close together ($<$ 10 cm apart) were considered as one individual to avoid clonal stems. Although we cannot be completely confident that all clones were excluded as roots were not excavated, we believe that this bias is minor and had little influence on our results, based on excavations of *Vismia* in other studies (Williamson et al. 1998). Species identification was made by comparison of collected specimens to specimens in the herbarium at the Instituto Nacional de Pesquisas da Amazonia (INPA). Details about each transect are presented in Table 1.

Although each vegetation type was conspicuously different in its floristic composition, we performed a nonmetric multidimensional scale (NMDS) analysis to objectively characterize each transect. We evaluated pairwise similarity in species composition among sites using the Chao-Jaccard abundance-based estimator (Chao et al. 2005). This estimator accounts for the effect of unseen species. In tropical forests, where rare species are frequent and the sampling is often incomplete, this index is less biased by sample size, and is therefore more appropriate that other similarity indices commonly used (Chao et al. 2005). We performed this analysis using data from the initial census, except for two transects that had very low stem densities, where we included the first census that had more than 30 individuals.

The NMDS showed a clear distinction between sites that were never burned or were burned only once, from sites that were burned more than once (Appendix 1). We characterized these as *Cecropia* and *Vismia* stands, respectively. Overall, 11 transects were classified as *Vismia* (total of 3700 m^2 sampled) and eight transects as *Cecropia* (total of 2700 m^2 sampled).

Although distance had a significant effect on the floristic similarity among transects (Mantel-test, $r = 0.2$, $p < 0.05$), the use of fire is likely to be the mayor determinant of the variation in species composition between forest types (Williamson and Mesquita 2001, Mesquita et al. 2001). The effect of distance might be the result of a spatial autocorrelation in land use rather than the result of dispersal limitation. For instance, the farm Esteio was converted to pasture from the road northward, so that the most inward transects were the least burned and are dominated by *Cecropia* (Fig. 2). Both vegetation types occurred within each farm; thus we believe that this spatial autocorrelation does not affect our results and further interpretations.

Statistical analyses

Comparing temporal changes in species richness and dominance between forest types

To assess changes in dominance over time in each of the two forest types, we calculated the indicator value metric (IndVal) of each species in each stand type (Dufrene and Legendre 1997). This statistic measures the ability of each species to discriminate among forest types by combining measures of habitat specificity (through data on relative abundance) and habitat fidelity (through presence–absence data). The metric varies between 0 and 1, and it is maximum when all individuals of a species are found in a single type of forest and when the species occurs in all sites of this forest type. We assessed the statistical significance of each species' IndVal by using a randomization procedure with 1000 iterations. Calculations were done using the function 'duleg' in the statistical package 'labdsv' (Roberts 2007) of the R statistical software.

Modeling frequency-dependence

For each transect, we assessed the strength and direction of frequency dependence by investigating changes in species relative abundance between the initial and the last census. Although censuses were realized yearly, few or no trees recruited or died each year, as transects were of small size. Given these low numbers, significant changes in species relative abundance were not detectable between consecutive censuses. Thus, we based our analyses on demographic changes between the initial and the last census to increase our statistical power. Also, we related initial relative abundance with relative abundance of recruited and dead individuals throughout the monitoring period of each transect. Frequency-dependence was evaluated by a power function of the following form:

$$f(x_i/\delta) = \frac{x_i^{\delta}}{\sum_i x^{\delta}} \tag{1}$$

where x_i is the relative abundance of species i at the initial census, and the dependent variable is either (1) the relative abundance of species i at the last census, (2) the relative abundance of species i among the cumulative number of recruits or (3) among the cumulative number of deaths over the monitoring period. The exponent δ differs significantly from zero when the power function provides a significantly better fit than a linear function. This exponent determines the sign and the strength of frequency-dependence. In cases (1) and (2), if δ is significantly greater than one, relatively abundant species are becoming even more abundant, indicating positive frequency dependence (Fig. 1a). If δ is significantly greater than zero but less than one, this indicates negative frequency dependence, where the more common species are reduced in frequency over time leading to a more even pattern in species frequency distribution – even if the species rank does not change (Fig. 1c). If δ is negative, species relative abundance shifts so that frequent species become rare species and vice versa, indicating strong negative frequency dependence (Fig. 1e). If δ is not different from one, species relative abundance remains constant over time, indicating that there is not frequency dependence (Fig. 1b). A fifth scenario is when δ is not significantly different from zero, in which case the dependent and independent variables are unrelated (Fig. 1d). Finally, in case (3), because the dependent variable considers dead individuals, the aforementioned considerations would be reversed.

We used maximum likelihood techniques to obtain the best-fit parameter estimates for δ in each transect and for each of the three dependent variables studied (relative frequency at the final census and cumulative recruited and dead individuals). Because our response variables were proportions, we assumed that they had a multinomial error distribution. Thus, the likelihood of the model parameter δ was calculated as:

$$L(\delta / x_i) = \frac{N!}{\prod_i n_i!} \times \prod_i \left(\frac{x_i^{\delta}}{\sum_i x_i^{\delta}} \right)^{n_i} \tag{2}$$

where N is the total number of individuals and n_i is the number of individuals of species i. We used asymptotic standard errors to evaluate the 95% confidence interval of the fitted parameters and to evaluate whether the values were significantly different from one (null model) or from zero (independence).

Results

A total of 748 stems of DBH ≥ 3 cm including 58 species belonging to 24 families were censused at the initial census in the *Vismia* transects, and 771 individuals including 222 species and 43 families were censused in the *Cecropia* transects. *Cecropia* transects had higher stem density than *Vismia* transects (2792 and 2021 stems ha^{-1} respectively). Over the subsequent censuses, *Vismia* sites recruited 629 individuals including 127 species and 36 families, 91 of which were new to the initial species pool; and 309 individuals died from 26 species of 13 families. *Cecropia* transects recruited 202 individuals including 129 species and

38 families, 56 of which were new to the initial species pool; and 163 individuals died from 38 species and 16 families.

Indicator value

Vismia transects presented only four species with significant indicator values, which were significant at both the initial and last censuses (*Bellucia imperialis*, *Goupia glabra*, *Vismia cayennensis* and *V. japurensis;* Fig. 3b). Thus, patterns of dominance did not change over the 8–10 year monitoring period. Among the 59 species present in the *Vismia* transects at either the initial or the last census, 31 showed an IndVal lower than 0.1, and most species points lie close to the diagonal, indicating little change between initial and last censuses. In contrast, *Cecropia* transects presented 13 species with significant indicator values at the initial census, and 14 at the last census (Fig. 3a). Of these, nine were significant at both the initial and last censuses. With the exception of *Trattinickia burserifolia* and *Eschweilera coriacea* – both species showing high indicator values at the initial and last censuses, species with high dominance at the initial census tended to decrease in frequency and abundance (e.g. *Guatteria oliveacea, Cecropia sciadophylla, Byrsonima chrysophylla*). Other species took over and showed higher indicator values at the last than at the initial census (*Protium hebetatum, Eschweilera grandifolia*). Overall, species indicator values in *Cecropia* transects showed a more scattered pattern, indicating that relative frequency in most species either increased or decreased between initial and last censuses.

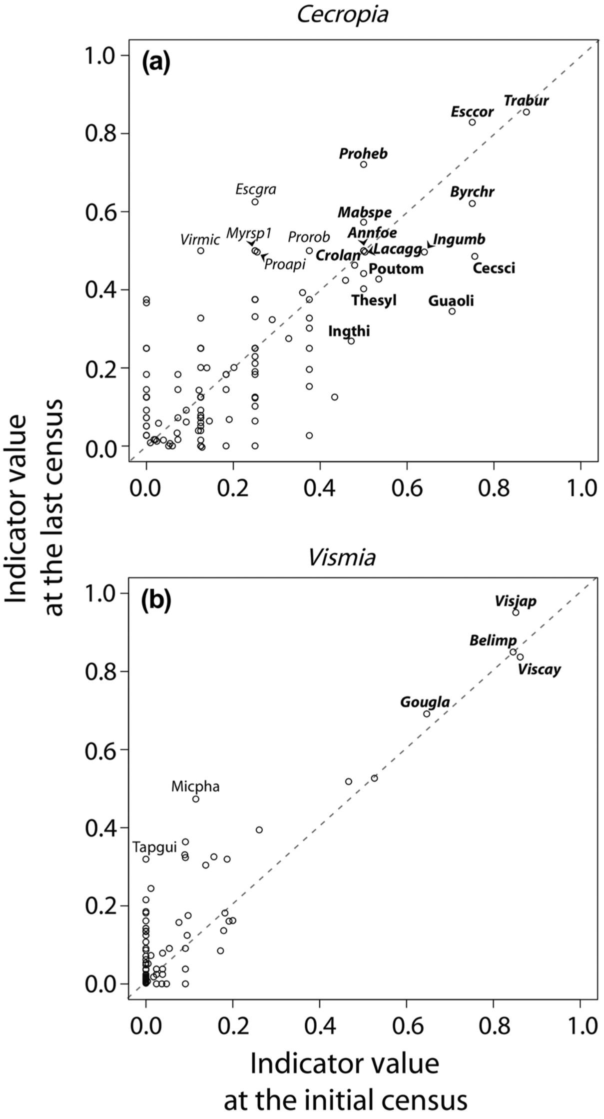

Figure 3. Changes in the indicator value of each species between the initial and the last censuses for *Cecropia* and *Vismia* stands. Species abbreviations correspond to the first three letters of the genus and species given in Table 2. Bold letters indicate species for which the IndVal was significant at the initial census and italic letters indicate species for which the IndVal was significant at the last census.

Frequency dependence

All *Vismia* transects showed a significant positive relationship between the initial and final species relative abundance (i.e. δ was significantly greater than zero; Fig. 4a). The exponent δ was significantly lower than 1 (negative frequency dependence) for eight out of 11 *Vismia* transects, and for the three remaining *Vismia* transects, relative abundance did not change over time (δ not significantly different from one). Among the eight *Cecropia* transects, seven showed significant positive trends ($\delta > 0$) and one showed no trend (δ not significantly different from zero) (Fig. 4a). The exponent δ was significantly lower than 1 (negative frequency dependence) for six transects, and for one the relation between initial and final species relative abundance was monotonic (δ not significantly different from one).

In terms of recruitment, *Cecropia* transects showed very strong negative frequency dependence (significantly negative values of δ) in five of the eight transects (Fig. 4b). In the three remaining *Cecropia* transects, the exponent δ was not significantly different from zero, although its sign was negative. *Vismia* transects, in contrast, showed negative frequency dependence in five transects out of 11, only one of which was very strong (Fig. 4b). Among the six remaining *Vismia* transects, four did not show any significant relationship between the relative abundance in recruits and initial relative abundance, and two showed a monotonic relationship between these two variables (δ not significantly different from one).

In terms of mortality, the relative abundance of dead individuals was significantly positively related with initial relative abundance for all transects, indicating that the most frequent species were those that were most likely to die (Fig. 4c). In all transects but two, the exponent δ was significantly greater than one indicating negative frequency dependence. Interestingly, these two exceptions corresponded to the two *Vismia* transects that showed a monotonic relationship between initial species frequency and frequency of recruited individuals, suggesting that frequency dependent processes are not regulating mortality and recruitment in these two transects.

Discussion

Although both types of forest showed negative frequency dependence, *Cecropia* stands showed a stronger and more consistent trend across transects. Vegetation dynamics were substantially slower in *Vismia* stands, where burning

Table 2. List of species that are referred to in the text and in the Fig. 3.

Species code	Species name	Family
Annfoe	*Annona foetida*	Annonaceae
Belimp	*Bellucia imperialis*	Melastomataceae
Byrchr	*Byrsonima chrysophylla*	Malpighiaceae
Cesci	*Cecropia scidophylla*	Urticaceae
Crolan	*Croton lanjouwensis*	Euphorbiaceae
Escgra	*Eschweilera grandiflora*	Lecythidaceae
Esccor	*Eschweilera coriacea*	Lecythidaceae
Gougla	*Goupia glabra*	Celastraceae
Guaoli	*Guatteria olivacea*	Annonaceae
Ingthi	*Inga thibaudiana*	Fabaceae
Ingumb	*Inga umbellifera*	Fabaceae
Lacagg	*Lacistema aggregatum*	Lacistemaceae
Mabspe	*Mabea speciosa*	Euphorbiaceae
Myrsp1	*Myrcia* sp. 1	Myrtaceae
Poutom	*Pourouma tomentosa*	Urticaceae
Proapi	*Protium apiculatum*	Burseraceae
Proheb	*Protium hebetatum*	Burseraceae
Prorob	*Protium robustum*	Burseraceae
Thesyl	*Theobroma sylvestre*	Malvaceae
Trabur	*Trattinnickia burserifolia*	Burseraceae
Virmic	*Virola michelii*	Myristicaceae
Viscay	*Vismia cayennesis*	Clusiaceae
Visjap	*Vismia japurensis*	Clusiaceae

had considerably affected the resilience of the system. These findings support several studies showing that repeated fires may cause stands to diverge from normal succession and attain an alternative state, resulting in a system exhibiting high resistance to species turnover (Mesquita et al. 1999, Hooper et al. 2004, Zarin et al. 2005). Such patterns arose from strong differences in frequency dependence during the recruitment process. In *Vismia* stands, species relative abundance of recruited individuals was positively correlated with initial species relative abundance in six out of the 11 transects studied, whereas this relationship showed a negative trend in all *Cecropia* transects. Thus, in *Cecropia* stands, frequent and abundant species are not only showing decreased performance in comparison to rare species, but they are also failing to recruit. Such compensatory recruitment will result in the sequential replacement of species observed throughout succession (Finegan 1996). In *Vismia* stands, in contrast, the most abundant species are still those that are recruiting the best. This positive feedback slows successional dynamics and leads the system to 'persistent-monodominance' (sensu Connell and Lowman 1989, Henkel et al. 2002). Lack or weak negative frequency dependence during the recruitment process is therefore the main source of resistance to the interchange of dominance between early- and late-successional species.

The dominance of *Vismia* species in *Vismia* stands arises because resprouting in these species seems to be stimulated by fire (Williamson and Mesquita 2001). Often, species that did not show any pattern of dominance possess specific traits enabling them to exhibit a positive response to a new regime of disturbance, resulting in an increased dominance of these species in the community (D'Antonio and Meyerson 2002). Indeed, *Vismia* species did occur in *Cecropia* stands but at low frequency and abundance, indicating that these species do not have invasive abilities per se, but that they outperform other early successional colonizers only under periodic burning. Such differential responses to different disturbance regimes suggest that the dominance exhibited by *Vismia* is the result of a competitive advantage associated with an earlier establishment. These priority effects could be overcome if the fire regime is interrupted, allowing the system to reverse from the alternative, persistent state to a more dynamic system (Young et al. 2001, Suding et al. 2004).

This conjecture is supported by the fact that, despite strong evidence of arrested succession, *Vismia* stands are gradually returning to a more even pattern in species relative abundance. Among the 11 transects monitored, eight showed negative frequency dependence in terms of stem density, five in terms of recruitment and eight in terms of mortality. Although, such regulation might be too weak to translate into a CCT at short time scales, the species frequency distribution among recruited individuals is becoming more balanced. We therefore expect the dominance of *Vismia* species to diminish over time – although this process is likely to be extremely slow, especially relative to natural succession in unburned clearcuts. Restoration efforts may help these degraded lands to disrupt the positive feedbacks that prevent normal succession (Dobson et al. 1997, Lamb et al. 2005). However, if fire is re-introduced into these pastures, any successional changes in these stands are likely to be set back (Hooper et al. 2004), and many of the restored forests will revert to monogeneric dominance by *Vismia* species. Moreover,

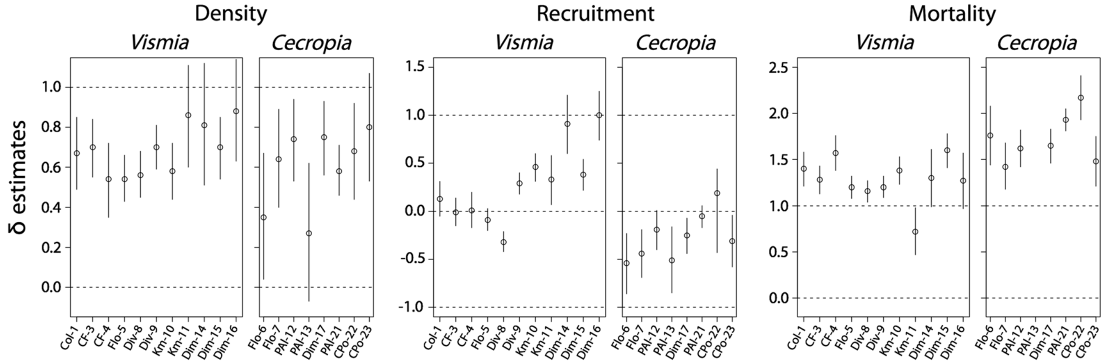

Figure 4. Parameter estimates of δ, the exponent determining the sign and the strength of frequency-dependence, and 95% confidence intervals for each of the transects. Parameters with estimates differ significantly from zero if the 95% CI do not overlap zero, and from one if the 95% CI do not overlap one.

once *Vismia* is firmly established, restoring original biodiversity or ecosystem functionality may require considerable time and financial investment, as these species are capable of self-replacement (Lamb et al. 2005, Chazdon 2008b).

The occurrence of alternative successional pathways dominated by *Vismia* species is not a local phenomenon. This genus is widely distributed across the Neotropics (Williamson and Mesquita 2001) and the use of fire for agricultural reasons is a common practice among local people (Zarin et al. 2005). *Vismia* dominance in burned clearcuts and abandoned pastures has been reported in several locations across the Amazon Basin, including the Bahia's coastal forests (Williamson and Mesquita 2001), near the Trombetas river in north Brazil (Parrotta et al. 1997), in French Guiana (Maury-Lechon 1991), in the upper Rio Negro in Colombia (Uhl 1987), and at the eastern Amazon (Uhl et al. 1988, Nepstad et al. 1990). Slow turnover in nutrient-poor soils such as those characterizing the Guyana Shield and eastern Amazonia (Phillips et al. 2004), combined with the presence of species characterized by traits adapted to low-dynamic environments (ter Steege et al. 2006) may contribute to the occurrence of these alternative successional pathways in the landscape. The *Cecropia*–*Vismia* system is an excellent example of alternative states and positive feedbacks that illustrate how priority factors associated with land-use may drive divergence in successional pathways. This case study provides the opportunity for the development of predictive tools helping to define recovery thresholds, and to determine the degree of resistance and resilience of a disrupted system (Young et al. 2001, Suding et al. 2004).

It could be argued that the distinct successional dynamics occurring in these two forest types might proceed from differences in age since abandonment. Because all the farms were clearcut at the same time (Mesquita et al. 2001), areas that were abandoned without any further land use and are therefore dominated by *Cecropia* are generally older than secondary stands dominated by *Vismia*. Yet, it is not likely that the pioneer species observed in the *Cecropia* stands could have established under the canopy of *Vismia* stands. To the contrary, *Vismia* stands that are four years older than those studied here, showed more *Vismia* and *Bellucia* at the expense of *Cecropia* and *Laetia* (Mesquita et al. 2001). Furthermore, species composition between *Vismia* and *Cecropia* stands is very distinctive, and largely independent of age since abandonment (Appendix 1). Thus, the occurrence of alternative successional dynamics reported here is not likely to be the result of different stages of succession, but rather is underlain by distinct processes driving the differential dynamics.

The CCT appeared to be an excellent framework to assess quantitatively successional dynamics in secondary forests, and sets the stage for the development of predictive tools critical in restoration ecology (Suding et al. 2004). Such advances are particularly important in species-rich communities, where the collapse of an ecosystem has major effects on biodiversity and ecosystem services (Lamb et al. 2005). Note that our approach does not provide a mechanistic understanding of the driving forces of successional dynamics: we cannot state that frequency dependent processes underlying the CCT are responsible for the alternative successional pathways observed in central Amazonia. Frequency dependence processes result from negative density dependence operating similarly among all the co-occurring species in an assemblage (Connell et al. 1984), and typically relies on host-specific natural enemies attacking locally abundant species (Janzen 1970, Connell 1971). In our study system the strong community compensatory trends observed in *Cecropia* stands are the result of functional variation among species belonging to different successional stages (Chazdon et al. 2010). In particular, differences in growth rates are one of the major drivers of successional dynamics (Gomez-Pompa and Vazquez-Yanez 1981, Finegan 1984, Chazdon 2008a). Thus, the predictive strength of frequency dependence processes we found does not necessarily imply causality (Doak et al. 2008), and other processes might be more directly responsible for the patterns observed.

Our novel approach is however an excellent framework in which to compare species turnover in secondary forests presenting alternative states, and is readily adaptable to other systems. As the extent of human-impacted landscapes increases across the globe, a better understanding of transition and stability models is very much in need. The development of appropriate predictors of ecosystem resilience is a large step toward this goal and will help in the identification of conservation priorities (Suding et al. 2004, Harvey et al. 2008). In this study, we contribute to this task by bringing a statistical tool helping to quantify and predict rates of change in community dynamics in sucessional forests. The use of quantitative criteria is particularly important for the development of restorative measures in successional communities exhibiting alternative pathways (Suding et al. 2004). Such efforts are critical to determine the degree to which degraded lands have the potential to safeguard species of high conservation value and sustain ecosystem services. Here, we addressed small-scale processes to characterize positive or negative feedbacks during successional dynamics, but an integrated understanding of successional patterns in a wide array of ecological systems also requires large-scale landscape manipulations.

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Appendix 1

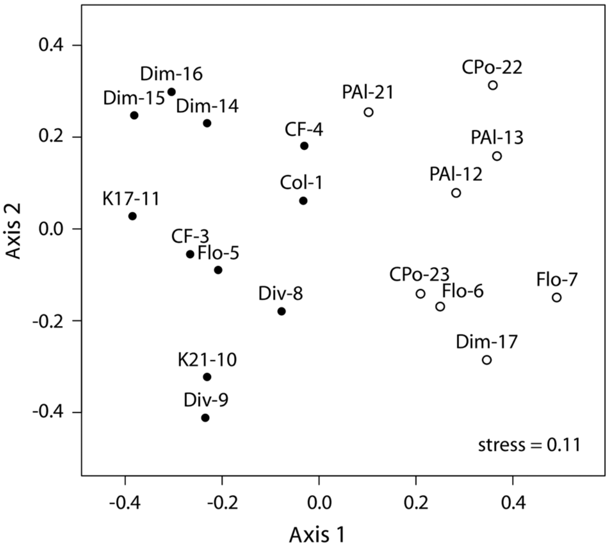

Figure A1. NMDS illustrating broad-scale compositional variation among transects. Floristic similarity among transects was calculated using the Chao–Jaccard estimator based index. Filled circles refer to transects that have been burned more that one time, and open dots refer to transects that have been burnt zero to one time.