



Land use as a filter for species composition in Amazonian secondary forests

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Keywords

Brazil; *Cecropia*; Fire; Landscape composition; Phosphorus; Slash-and-burn; Soil; Sprouting; Succession; *Vismia*; α -Diversity; β -Diversity

Abbreviations

SF = Secondary forests.

Nomenclature

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Introduction

Under the current high rates of land-cover change in the tropics, secondary forests have expanded in area and have

Abstract

Questions: Secondary succession in the tropics can follow alternative pathways. Land-use history is known to engender alternative successional communities, but the underlying mechanisms driving and sustaining divergence remain unclear. In this study we aim to answer the following questions: (1) does previous land use act as a filter for species composition in secondary forests; and (2) what are the relative roles of management practices, soil properties and landscape composition in determining species composition?

Location: Central Amazon, Brazil.

Methods: We sampled trees, shrubs and palms (≥ 1 cm diameter) in 38 early secondary forests (5 yr after abandonment) located along gradients of land-use intensity in five shifting cultivation landscapes. We measured the diameter and height of each sampled plant, identified it to species or morpho-species level and checked if it was resprouting or not. At each secondary forest we also collected soil samples for chemical and physical analyses and estimated the amount of old-growth forest surrounding it (landscape composition).

Results: We found that previous land-use intensity determined species composition. With increasing land-use intensity, management practices of cut-and-burn and associated reduction in soil quality filtered out seed-dependent species and favoured strong sprouters and species that can cope with low nutrient availability. Landscape composition had a weak effect on species assemblages. We found specific species assemblages and indicator species associated with different levels of previous land-use intensity. As a consequence of these local filters, species α - and β -diversity decreased and therefore early successional communities became more similar to each other.

Conclusion: Species composition of successional forests is strongly determined by different land-use intensities. Dispersal limitation has a limited effect on determining the composition of the dominant species. Filtering effects of management practices and soil quality determine the species dominating the canopy at early stages of succession and narrow down the range of species able to colonize and establish. This study highlights how land use shapes successional communities and suggests that alternative successional pathways are determined at early stages of succession. Therefore, accounting for land-use history is crucial to improve the understanding of tropical secondary succession. We present a list of indicator species for different levels of previous land-use intensity that can be used to support conservation and restoration decisions in the Amazon.

become more important in the biodiversity conservation and ecosystem services agendas. Studies have shown, however, that secondary forests do not form a homogeneous category since regrowth rates and species

compositions are highly variable across and within sites (Chazdon 2008; Norden et al. 2015). An intricate set of factors influence species composition of secondary forests, such as successional age (Finegan 1996; Peña-Claros 2003), dispersal limitation (Holl et al. 2000; Cubiña & Aide 2001; Robiglio & Sinclair 2011), soil properties (Lawrence 2005; Powers et al. 2009), land-use history (Mesquita et al. 2001; Longworth et al. 2014) and biotic interactions with remnant vegetation and invasive species (Slocum 2001; Hooper et al. 2004; Walker et al. 2010a). Given the prevalence of land-use change in the tropics, understanding how previous land use shapes successional communities is crucial to elucidate tropical forest succession in human-modified landscapes (Arroyo-Rodríguez et al. 2015).

Previous land-use history has been associated with alternative successional pathways characterized by distinct species composition and rates of change (Mesquita et al. 2001, 2015; Norden et al. 2011). Different processes have been evoked to explain how land use drives the alternative pathways, such as abiotic filtering, dispersal limitation, priority effects and species interactions (Norden et al. 2011; Mesquita et al. 2015). The broadly termed 'land use effect', however, is mediated by concomitant effects of landscape composition (proportion of different land cover types in the landscape), management practices and soil properties, which have rarely been jointly assessed (Aragón & Morales 2003; Lawrence 2005; Robiglio & Sinclair 2011). Accounting for variations in these three factors is, therefore, essential to elucidate the mechanisms underlying land-use effects.

Land-use changes are usually followed by land-cover changes such as deforestation, forest fragmentation and decreased permanence of old-secondary forests in the landscape (Lawrence et al. 1998; Metzger 2002; van Breugel et al. 2013). Such land-cover changes may enhance species dispersal limitation in human-modified landscapes (Robiglio & Sinclair 2011; Arroyo-Rodríguez et al. 2015) and determine the species able to first colonize and subsequently dominate new open sites. In the wet tropics, where slash-and-burn practices prevail, the number of cut-and-burn events a field had been subjected to determines vegetation structure and regrowth rate of secondary forests regenerating after cattle ranching (Zarin et al. 2005) and shifting cultivation (Jakovac et al. 2015). In a previous study we have shown that such practices led to an increase in the percentage of resprouting individuals (genets) in successional communities (Jakovac et al. 2015). Consequently, by favouring species with traits like high sprouting ability and fire-resistant seeds, such slash-and-burn practices can induce a shift in species composition (Hooper et al. 2004). Simultaneously, previous land use affects soil conditions by depleting nutrients and

changing physical properties (Palm et al. 1996; Lawrence et al. 2007; Runyan et al. 2012; Jakovac et al. 2015). Although it remains unclear how soil properties affect species composition in successional forests, the distribution of many tropical species has been shown to depend on nutrient availability (John et al. 2007; Toledo et al. 2012; Condit et al. 2013). These factors underlying land use could, therefore, act as ecological filters selecting for specific traits and restricting the range of successful species able to establish at new open sites (Lortie et al. 2004).

In this study we aimed to elucidate how previous land use shapes successional communities, evaluating whether the variation in species composition across the landscape is a result of filtering processes imposed by land use and mediated by management practices, soil quality and landscape composition. If land use acts as a filter on the local species pool, we expect to find a directional change in species traits and composition and an increase in the similarity among plant communities, i.e. a reduction in β -diversity with increasing land-use intensity. To test this hypothesis, we (1) first assessed the roles of management intensity, soil quality and landscape composition in determining species composition of early secondary forests, and (2) tested if there were indicator species associated with specific environmental/land-use conditions. We then (3) evaluated if such species–environment relationships were associated with a selection for strong sprouter species and (4) with a reduction in the α - and β -diversity of secondary forests.

We used a novel sampling design, where successional age was kept constant across sites (ca. 5 yr after abandonment) and sites were located along gradients of land-use intensity. We focused on early stages of succession, when a few species dominate the canopy and the effects of previous land use have not been attenuated by other environmental changes through successional age. The early species that form the canopy during the first ca. 20 yr of succession (Finegan 1996) regulate environmental conditions in the understorey (Kabakoff & Chazdon 1996; Lebrija-Trejos et al. 2011; Jakovac et al. 2014) and important biotic interactions (Walker et al. 2010a; Maggi et al. 2011) that may affect further species turnover. Therefore, elucidating how land use shapes early communities is essential to improve the understanding of tropical secondary succession.

Methods

Study site

The study was carried out in the region of the middle Amazon River in the municipalities of Tefé and Alvarães, Amazonas State, Brazil. The landscape in this region has been mainly transformed by cultivation of cassava in shifting cultivation systems (also known as swidden-fallow

systems). Agriculture is practiced by smallholder farmers, in cropping fields of 1–3 ha, based on family and collective labour (Jakovac et al. 2016). Study sites are located on non-flooded areas (*terra firme*) over soils classified as oxisols and ultisols in USDA soil classification and as ferrasol and acrisol in the World Soils Reference database (WRB 2014). Soils are generally acid, with high aluminium content and low base saturation (Jakovac et al. 2015).

Data collection

We sampled, in 2012 and 2013, 38 early secondary forests (SF) in five villages, Agrovila (ten SF), Nogueira (11 SF), Vila São (six SF), São Francisco (six SF) and São Sebastião (five SF), which were 3–66 km apart from each other (Fig. 1). We did not use a chronosequence approach to avoid successional age effects and to be able to focus on the effects of land use itself on early plant communities. Sampled SF had an age after abandonment of 5 ± 0.1 (SE) yr, and were subjected to varying degrees of land-use intensity. We selected SF to be sampled according to their management intensity history, soil characteristics (colour and texture) and distance to the old-growth forest. By sampling

in different villages and searching for variation in these three factors within villages we have covered the variation in our study landscape.

Management intensity was defined by the following practices: number of swidden-fallow cycles, number of weeding events during the previous cropping period, age of the previous fallow and the current area of the SF patch. We selected for SF regrowth on sites that had been used for one up to ten swidden-fallow cycles. We assessed the land-use history of every SF by interviewing landowners and their families (for details on questionnaires see Jakovac et al. 2015).

To characterize soil quality, we collected one composite soil sample at every SF, composed of five samples taken from the upper 20 cm using a bucket auger, randomly located in the plot. Samples were air-dried and taken to the EMBRAPA soil laboratory for chemical (soil organic C, total N, available P [Mehlich-1], exchangeable K, Ca, Mg, Al, extractable Fe, and pH) and texture analysis, following published protocol (EMBRAPA 2011). Landscape composition was defined as the area covered by old-growth forest within a 500-m radius surrounding each SF patch (79 ha area). We chose this metric of landscape composition

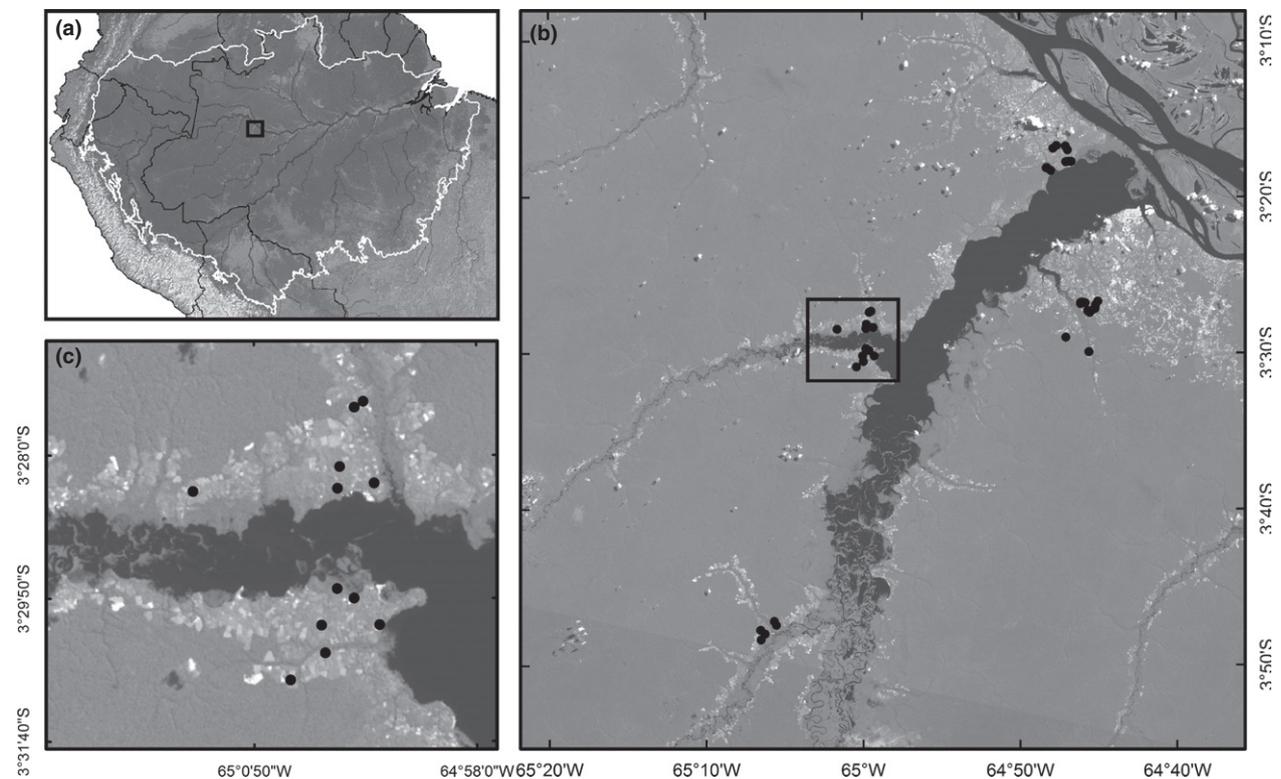


Fig. 1. Location of study area and sampled secondary forests. (a) Location of the study region (black square) in the Amazon Basin (white line) in South America. (b) Landsat image (2015) of the study region, representing bare soil and urban areas in white, agricultural areas in light grey and old-growth forest in dark grey. Black dots indicate locations of the secondary forests sampled in five different villages distributed along the Tefé River. (c) Zoomed area indicated by the black square in (b), showing distribution of sampled secondary forests in two villages.

because the amount of habitat in the local landscape has been suggested as a comprehensive proxy for patch size and isolation, which can be associated with ecological processes such as dispersal limitation (Fahrig 2013). We selected the 500-m radius based on the strength of the relationship between different radius length and species richness (Appendix S1). We overlaid the SF patch locations, acquired with a GPS in the field, with a land-use-cover classification map provided by PRODES (INPE 2011) and calculated the area covered by old-growth forest within a 500-m radius around each SF. Measurements were done in ArcGIS 10.1 (Environmental Systems Research Institute, Redlands, CA, US). For detailed methodology see Jakovac et al. (2015).

To characterize plant species composition, at each SF we located a 50-m-long transect line where we sampled trees, palms and shrubs at two different widths: individuals (genets) with DBH ≥ 5 cm in 50 m \times 10 m transect, and genets 1–5 cm DBH in 50 m \times 5 m transect. For every sampled genet we checked whether or not it was a resprout, considering it as a resprout when stems were clearly regenerating from a stump or when they were connected to roots at the soil surface. Stems from the same species that were ≤ 50 cm apart were also considered as belonging to the same genet, which we confirmed by excavating in some cases. This is a conservative criterion, given that clonal species can resprout beyond this threshold. For all stems we measured DBH, estimated height and identified to species or morphospecies. Plants that could not be identified in the field were collected and taken to the herbarium of the Instituto Nacional de Pesquisas da Amazônia-INPA, in Manaus, Brazil, and were then identified with assistance from an experienced para-taxonomist.

Statistical analyses

To evaluate how management intensity, soil properties and landscape composition shape species composition of early secondary forests, we applied a multivariate regression tree (MRT) on species composition weighted by basal area (i.e. the number of individuals of each species multiplied by its basal area in each SF plot). We weighted species by basal area to give more importance to the most dominant species and individuals, which are those forming the canopy of young secondary forests. All sampled individuals from both DBH classes were included in the analyses. We included as environmental variables all descriptors of management practices, soil quality and landscape composition. In preliminary analysis descriptors of geographic location (x and y coordinates and the corresponding polynomials) of each SF were also included as independent variables to evaluate possible effects of spatial autocorrelation in species composition. Because descriptors of geographic

location were not selected by the MRT, we performed the analysis again excluding geographic location. MRT is a type of constrained cluster analysis that groups samples (plots) to minimize differences (in both species composition and environmental variables) within groups and maximize differences among groups (De'ath 2002). Accordingly, the MRT analysis groups together plots that have similar species composition and similar environmental properties. MRT is a multivariate analysis especially suited for identifying and modelling species–environment relationships while including higher-order interactions (De'ath 2002). We based the MRT on the sum of squares, allowing a minimum of four sites in the final groups or 'leaves'. Model selection was based on cross-validation, with the best model/tree having the lowest number of leaves and estimated error (De'ath 2002). Additionally we compared the amount of species variance explained by constrained (MRT) and unconstrained cluster to evaluate the efficiency of the MRT in determining community types.

After selecting the best tree, we calculated the indicator value for each species in each group formed by the MRT, to evaluate whether species were significantly associated with a particular group. Indicator species are defined as the most characteristic species of a group, found exclusively or more frequently in a single group of sites and present in the majority of the sites of that group (Dufrene & Legendre 1997).

Next, we evaluated how the groups of secondary forests formed by the MRT also differed in plant functional traits (percentage of resprouting individuals and of strong sprouter species) and species diversity (both α - and β -diversity). Percentage of resprouting individuals at each SF was calculated as the proportion of resprouting genets to the total number of genets. We calculated the percentage of strong sprouter species at each SF as the proportion of strong sprouter species to the total number of species. We considered a species as strong sprouter when $\geq 60\%$ of its individuals were sprouting over the whole data set, considering only species with more than ten individuals sampled. The MRT groups were compared using ANOVA followed by Tukey pair-wise comparisons, at a level of significance of 0.05. Prior to analyses we tested whether the response variables follow a normal distribution and have homogeneity of variance across MRT groups.

α -Diversity was calculated as the species richness at each SF plot (500 m²) and as the rarefied species richness, to take into account differences in density of individuals, although sample coverage was similar across groups (Appendix S1; Chao & Jost 2012). We tested the differences in α -diversity among MRT groups with a GLM using Poisson distribution. We assessed β -diversity as the variability in species composition among SF plots within each MRT group, also called multivariate dispersion (Anderson

et al. 2006). Samples were ordered using a PCA based on Jaccard similarity index. Then, the average distance from each individual sample (plot) to its group centroid in the multivariate space was calculated (Anderson et al. 2006). A larger distance indicates higher dispersion of samples within a group, and therefore, higher β -diversity. Pair-wise comparisons of β -diversity among MRT groups were performed with a permutation test with 999 permutations.

Analyses were performed using the R-Studio interface to R (R Foundation for Statistical Computing, Vienna, AT), using the following packages: *mvpwrap* for MRT, *indic-species* for indicator species analysis, *vegan* (*betadisper* and *rarefy* functions) for species diversity, *glm2* for GLM and *car* for ANOVA analyses. Percentage values (resproutings, strong sprouters, clay and silt) were transformed by the arcsine of the square root prior to analyses.

Results

We sampled a total of 7373 individuals belonging to 280 species, 153 genera and 54 families including trees, shrubs and palms with DBH ≥ 1 cm. Half of the species occurred occasionally, with 138 species being singletons or doubletons. The most common 23 species were responsible for

80% of the total basal area and were usually those at the canopy layer. Most species had at least one individual resprouting (178 species) but only 30 species were classified as strong sprouters.

Determinants of species composition

The MRT analysis indicated that number of swidden-fallow cycles, clay content and P availability determined species composition (Fig. 2). The best MRT had four leaves (groups) and explained 34% of the total species variance. Constrained MRT had 84% efficiency when compared to the unconstrained cluster, which explained 41% of total species variance. Such high efficiency indicates that most of the important factors affecting species distribution were taken into account in this study.

The first split of the MRT was determined by number of swidden-fallow cycles, and accounted for 47.3% of the explained species variance. This first split grouped together all six SF plots that were subjected to only one swidden-fallow cycle (one-cycle group – Cy). The second split was determined by clay content, and explained an additional 28.4% of the explained species variance, grouping seven SF plots that were located on soils containing $\geq 22\%$ clay

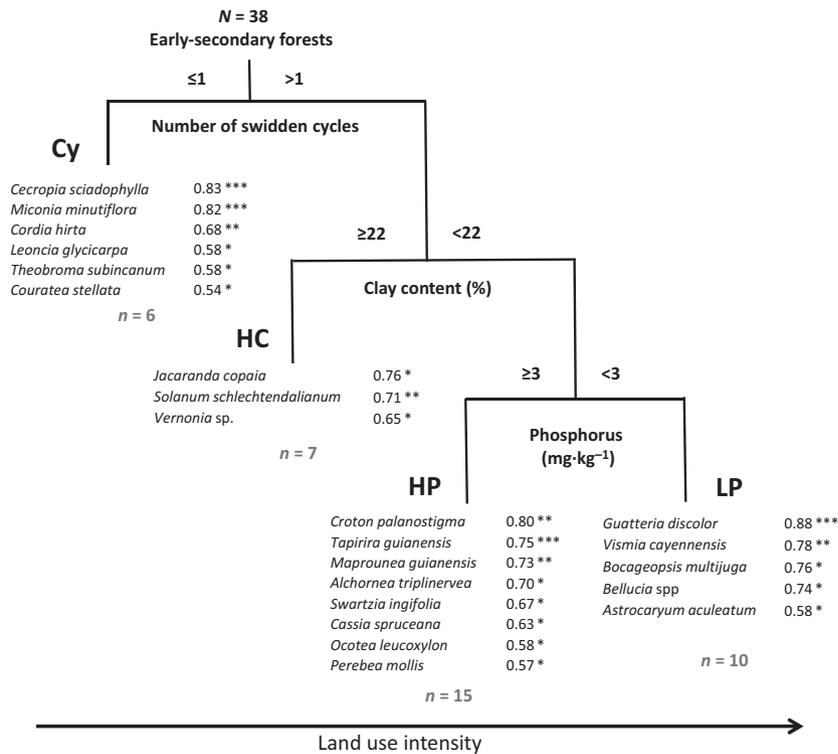


Fig. 2. Multivariate regression tree of species composition of 38 secondary forests in Brazil (total of 280 species). At each ‘leaf’ of the tree, a name is given to the group: Cy – one swidden cycle; HC – high clay; HP – high P and LP – low P. At each leaf all significant indicator species are listed, followed by their respective indicator value and level of significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$), and number of secondary forest plots clustered in each group (n). The groups of the MRT are ordered according to land-use intensity, which increases from left to right.

(high clay group – HC). The final split, which accounted for the remaining 24.3% of the explained species variance, was determined by P availability in the soil. This split grouped together ten SF plots that were located on soils with $<3 \text{ mg}\cdot\text{kg}^{-1}$ available P (low P group – LP). The remaining 15 SF were grouped under the relatively high P group (HP; $\geq 3 \text{ mg}\cdot\text{kg}^{-1}$). These four groups of secondary forests represent distinctive associations of species assemblages and environmental conditions (Table 1).

Species–environment relationships: indicator species

The four groups defined by the MRT were characterized by 22 indicator species (Fig. 2, Table 2). Four indicator species occurred exclusively in one group, three of them being associated with the one-cycle group (Cy). Eighteen species were assigned as indicator due to their higher frequency and abundance in one of the four groups (Table 2). The Cy group contained six indicator species, among which *Cecropia sciadophylla* Mart. (Urticaceae) and *Miconia minutiflora* DC. (Melastomataceae) had the highest indicator values. *Cecropia sciadophylla* was the dominant species, constituting 42% of the basal area in this group (Table 2). The HC group contained *Jacaranda copaia* (Aubl.) D. Don (Bignoniaceae), *Solanum schlechtendalianum* Walp. (Solanaceae) and *Vernonia* sp. (Asteraceae) as indicator species. *Jacaranda copaia* was the dominant species, with 32% of the basal area (Table 2). *Solanum* and *Vernonia* had relatively high

numbers of individuals but very low basal area (Table 2), as they are typical understorey shrubs achieving 3 m in height on average. The LP group contained five indicator species, with *Guatteria discolor* R.E.Fr. (Annonaceae) and *Vismia cayennensis* (Jacq.) Pers. (Hypericaceae) having the highest indicator values. *Vismia cayennensis* was the dominant species in this group (23% of the basal area; Table 2). The remaining group (HP) was characterized by eight species, with *Croton palanostigma* Klotzsch (Euphorbiaceae) and *Tapirira guianensis* Aubl. (Anacardiaceae) as the strongest indicators (Fig. 2). *Croton palanostigma* and *Cassia spruceana* Benth. (Fabaceae) were the dominant species in this group (Table 2).

Species diversity and plant functional traits

The groups formed by the MRT were significantly different in α - and β -diversity as well as in the percentages of resproutings and strong sprouter species (Fig. 3). These characteristics of the plant community showed a consistent trend of change following the MRT grouping, in agreement with the decline in soil quality and increase in number of cycles (Table 1). Secondary forests within the Cy group had a higher number of species and were more dissimilar than the secondary forests within the LP group (for α -diversity: $F_{3,34} = 5.18$, $P = 0.004$; for β -diversity: $F_{3,34} = 4.03$, $P = 0.015$; Fig. 3a,b). When controlling for differences in sample size (Appendix S1), the difference in

Table 1. Characteristics of the four groups of secondary forests formed by the multivariate regression tree (Fig. 2).

Environmental variables	Cy	HC	HP	LP
Management Practices				
Number of Cycles	1.00 (–)	2.71 (1.11)	4.27 (2.01)	5.70 (1.88)
Previous Fallow Period (yr)	> 70 (–)	3.79 (1.03)	4.13 (0.88)	4.30 (1.08)
Number of Weedings	1.33 (0.47)	2.07 (0.56)	2.63 (0.56)	2.85 (0.55)
Landscape Composition				
Area of Old-Growth Forest (ha)	0.38 (0.22)	0.14 (0.15)	0.04 (0.07)	0.03 (0.08)
Soil Properties				
Clay (%)	24 (9)	26 (5)	13 (5)	15 (3)
Silt (%)	33 (11)	33 (5)	33 (12)	34 (9)
Sand (%)	43 (16)	41 (8)	54 (16)	51 (8)
pH	3.61 (0.12)	3.68 (0.12)	3.59 (0.16)	4.05 (0.22)
C ($\text{g}\cdot\text{kg}^{-1}$)	18.41 (3.85)	19.81 (4.54)	17.61 (6.21)	14.60 (3.25)
N ($\text{g}\cdot\text{kg}^{-1}$)	1.51 (0.41)	1.57 (0.23)	1.37 (0.43)	0.99 (0.19)
P ($\text{mg}\cdot\text{kg}^{-1}$)	2.67 (1.21)	2.14 (0.90)	4.40 (1.54)	1.50 (0.53)
K ($\text{cmol}_c\cdot\text{kg}^{-1}$)	0.08 (0.01)	0.08 (0.01)	0.07 (0.02)	0.07 (0.02)
Fe ($\text{mg}\cdot\text{kg}^{-1}$)	267.33 (94.56)	255.57 (68.32)	250.27 (65.13)	345.60 (96.50)
Ca ($\text{cmol}_c\cdot\text{kg}^{-1}$)	0.08 (0.02)	0.09 (0.03)	0.06 (0.03)	0.04 (0.01)
Mg ($\text{cmol}_c\cdot\text{kg}^{-1}$)	0.19 (0.08)	0.17 (0.02)	0.13 (0.04)	0.14 (0.07)
Al ($\text{cmol}_c\cdot\text{kg}^{-1}$)	5.26 (1.54)	4.97 (0.76)	4.15 (1.15)	4.01 (0.69)
CEC ($\text{cmol}_c\cdot\text{kg}^{-1}$)	5.63 (1.64)	5.33 (0.83)	4.42 (1.25)	4.27 (0.76)
Sum of Bases ($\text{cmol}_c\cdot\text{kg}^{-1}$)	0.37 (0.10)	0.35 (0.04)	0.27 (0.08)	0.27 (0.09)

Means and SD of the environmental variables are provided. MRT groups abbreviation stands for Cy – one swidden cycle; HC – high clay; HP – high P and LP – low P.

Table 2. List of indicator species of the groups formed in the multivariate regression tree (Fig. 2).

Indicator Species	Total Genets	Relative Basal Area (%)				Resproutings (%)				
		Cy	HC	HP	LP	Total	Cy	HC	HP	LP
One cycle (Cy)										
<i>Cecropia sciadophylla</i>	244	41.8	12.7	1.3	0.8	4.5	4.7	2.9	–	6.3
<i>Miconia minutiflora</i>	8	0.4	–	–	–	25.0	33.3	–	–	–
<i>Cordia hirta</i>	5	0.3	–	–	<0.1	40.0	16.7	–	–	100.0
<i>Theobroma subincanum</i>	2	<0.1	–	–	–	–	–	–	–	–
<i>Leoncia glycyarpa</i>	3	0.1	–	–	–	100.0	100.0	–	–	–
<i>Couratea stellata</i>	7	0.1	<0.1	<0.1	–	85.7	83.3	100.0	100.0	–
High Clay (HC)										
<i>Jacaranda copaia</i>	536	6.5	31.8	1.1	10.5	11.4	0.6	4.5	38.5	18.9
<i>Solanum schlechtendalianum</i>	79	0.2	0.4	<0.1	<0.1	46.8	23.2	36.4	83.3	100.0
<i>Vernonia</i> sp.	52	<0.1	1.5	–	<0.1	61.5	100.0	74.5	<0.1	100.0
High Phosphorus (HP)										
<i>Croton palanostigma</i>	244	–	0.7	10.9	0.2	21.3	–	–	21.0	28.6
<i>Cassia spruceana</i>	194	0.4	1.4	7.1	0.6	79.9	–	25.0	80.5	87.5
<i>Tapirira guianensis</i>	17	0.1	–	1.4	0.1	64.7	–	–	87.0	–
<i>Maprounea guianensis</i>	71	0.1	0.2	0.8	0.1	66.2	16.7	28.6	70.2	35.0
<i>Alchornea triplinervea</i>	31	0.2	–	2.0	0.5	25.8	–	–	28.4	25.0
<i>Swartzia ingifolia</i>	18	<0.1	0.1	0.8	–	66.7	–	100.0	76.2	–
<i>Perebea mollis</i>	13	<0.1	–	0.2	–	61.5	100.0	–	55.3	–
<i>Ocotea leucoxydon</i>	26	–	–	3.2	–	30.8	–	–	24.1	–
Low Phosphorus (LP)										
<i>Vismia cayennensis</i>	986	3.2	8.3	4.9	23.4	62.8	13.2	18.4	51.2	62.2
<i>Gutteria discolor</i>	55	<0.1	0.1	<0.1	0.6	70.9	–	58.3	100.0	73.5
<i>Bellucia</i> spp.	170	1.5	1.2	0.1	3.9	18.8	6.3	5.2	–	15.2
<i>Bocageopsis mutijuga</i>	169	0.5	0.3	0.7	2.7	69.2	37.3	95.2	96.4	97.8
<i>Astrocaryum aculeatum</i>	7	–	–	0.6	4.3	0.0	–	–	–	–

For each species, we present the total number of individuals sampled (total genets); relative basal area at each MRT group (Cy, HC, HP and LP), and percentage resprouting genets within the whole data set (Total) and within each MRT group (Cy, HC, HP and LP). Values in bold indicate the indicator species group association. Absence of the species in the sample is represented by (–).

species richness between Cy and LP decreased and became marginally significant (for rarefied species richness to 92 individuals: $F_{3,34} = 2.73$, $P = 0.058$; Appendix S2), probably following the reduction in number of single and doubletons (Appendix S1), which are the rare species that mainly contribute to species richness in young secondary forests (Wieland et al. 2011). The groups HC and HP had intermediate levels of diversity and, in general, did not differ from each other. The percentage of resproutings was significantly lower in the Cy and HC groups than in the HP and LP groups ($F_{3,34} = 34.7$, $P < 0.001$; Fig. 3c). This pattern was also apparent at the species level, with the percentage of strong sprouter species increasing in the following order: Cy < HC < HP < LP ($F_{3,34} = 19.7$, $P < 0.001$; Fig. 3d, Table 2).

Discussion

In our study we showed that land-use intensity determines species composition and species diversity through a hierarchy of filters acting at early stages of succession and

selecting for strong sprouter species. Such filtering effects are mediated by management practices and soil properties and result in reduced α - and β -diversity, homogenizing successional communities across the landscape. Our results indicate that land use is responsible for creating and likely maintaining alternative successional pathways by modifying initial site conditions.

Determinants of early successional species composition

Our analysis showed that the effect of land use on species composition was mediated by a hierarchy of factors, where number of previous swidden-fallow cycles emerged as the primary determinant, followed by clay content and P availability. An earlier study provided evidence that soils become less clayey and lost basic cations with repeated swidden-fallow cycles (Jakovac et al. 2015, 2016). In the present study, the SF grouped by high clay content (Cy and HC groups) had been subjected to lower intensity of use (one to three swidden-fallow cycles), and SF from the HP and LP groups had been subjected to more than three

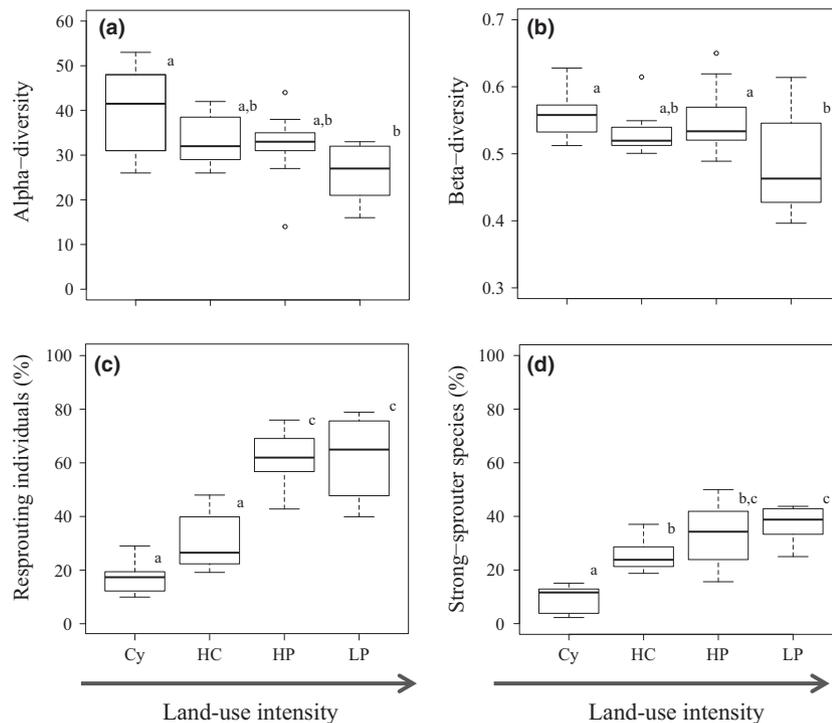


Fig. 3. Changes in community diversity and regeneration strategies with previous land-use intensity. Comparisons across MRT groups on (a) α -diversity calculated as number of species within 500 m², (b) β -diversity, (c) percentage resprouting genets and (d) percentage strong sprouter species, for each group formed by the multivariate regression tree. Cy (one cycle), HC (high clay content), HP (high P content), LP (low P content). Boxes represent lower and upper quartile, horizontal line represents the median, and whiskers extend to the lowest and highest datum within 1.5 interquartile range. Significant differences among groups are indicated with different letters.

cycles (Table 1). Hence, the species composition patterns reported here must be interpreted as resulting from the interaction between increasing number of cycles and decreasing soil quality (Table 1).

The relation between soil properties and species composition has seldom been evaluated in secondary forests, and results varied from soil properties strongly determining species composition (Aragón & Morales 2003; Powers et al. 2009) to soil properties having no significant effect (Lawrence 2005; Gomes & Luizão 2012). This contrast may be partly due to high plot-to-plot variability in species composition and in soil quality of SF, combined with the dominant chronosequence sampling design, where successional age may override local differences in soil properties (Feldpausch et al. 2004, 2007). Our sampling design, in which we explicitly excluded the effect of successional age, allowed for higher detectability of the effect of soils on the plant community.

The lack of effect of landscape composition on the composition of early successional species agrees with other studies (Guariguata et al. 1997; Holl et al. 2000; Benítez-Malvido et al. 2001; Reid et al. 2014). Dispersal limitation has been shown to be more important for determining the diversity of old-growth forest species

regenerating in the understorey of secondary forests than of common pioneer species (Guariguata 2000; Wieland et al. 2011). Landscape composition, therefore, may play a more important role in determining species composition at later stages than at early stages of succession (Reid et al. 2014; Craven et al. 2015), when old-growth forest species replace the widespread pioneers. Early pioneer species have small seeds that are dispersed across distances by birds, bats and wind, and form long-lasting seed banks (Reid et al. 2014). These characteristics guarantee a wide distribution within and across landscapes, which was also detected in our data set showing the same dominant species occurring at the five sampled villages. The fact that SF located at different villages were grouped by descriptors of previous land-use intensity indicates that land use was stronger than geographic location in determining species composition. These results were also observed in preliminary analyses (results not shown) in which descriptors of geographic location (x and y coordinates and their polynomials) were not selected by the MRT and did not take the place of management practices or soil properties in grouping the SFs. Hence, our study supports that the composition of the dominant species in young secondary forests is

unrelated to dispersal limitation and is mainly a result of changes in local site conditions mediated by land use.

Species–environment relationships and the role of sprouting ability

Evaluating the relationships between indicator species and environmental/land-use factors can help explain the mechanisms underlying shifts in species composition (De'ath 2002). Most indicator species were widely distributed across the sites but achieved higher relative basal area under specific environmental/land-use conditions (Table 2), indicating that the species favoured by land-use intensity were a subset of the regional species pool (Table 2), rather than exogenous species that could invade and dominate degraded lands (Schneider & Fernando 2010). In agreement with our hypothesis, the shift in species composition was associated with a selection for strong sprouter species (Fig. 3, Table 2). Although most tropical forest species are able to resprout (Kauffman 1991; Poorter et al. 2010), only a few can resprout after repeatedly losing its above-ground biomass (Bond & Midgley 2001; Hooper et al. 2004).

The species associated with low land-use intensities (≤ 3 cycles) and higher soil quality (Table 1, Fig. 2), *Cecropia sciadophylla* and *Jacaranda copaia*, are fast-growing pioneers (Popma & Bongers 1988) that reached approximately 16 m in height in 5 yr of succession. These species are poor resprouters (Table 2), susceptible to repeated cutting and burning practices, and may require relatively high nutrient availability to support their high growth rates (Gomes & Luizão 2012). *C. sciadophylla* seems to be especially susceptible to such practices, exclusively dominating one-time-burned areas in our and other studies in the Amazon region (Steininger 2000; Mesquita et al. 2001; Peña-Claros 2003; Hooper et al. 2004). Differences in Cy and HC species composition could also be a result of germination requirements. Some seeds may need long-term full sunlight to germinate (Popma & Bongers 1988), which condition is only achieved in the first cycle when the seed bank is mainly composed of trees and the ground takes longer to be fully covered by vegetation, while in subsequent cycles herbs and weeds cover the ground faster (Jakovac et al. 2016), possibly shading out seeds from light-demanding tree species. Controlled experiments on very early colonization, pioneer species germination and interspecific competition for light are needed to further disentangle the mechanisms underlying the effects of land use on species composition.

The two species associated with intermediate levels of land-use intensity and soil quality, *Croton palanostigma* and *Cassia spruceana* (Table 1, Fig. 2), are slower growers than *C. sciadophylla* and *J. copaia*, achieving around 9 m in

height in 5 yr of succession. These species are favoured by land-use intensification due to their capacity to resprout (Table 2), but may not be able to cope with extremely low P availability, like *Guatteria discolor*, *Vismia cayennensis* and other species from the LP group. This finding is in line with broad-scale studies showing an important role of soil properties, and specifically of P availability (Condit et al. 2013), in the distribution of tropical rain forest species (John et al. 2007; Dalling et al. 2012; Toledo et al. 2012). The dominant species at sites with extremely low P availability, *Vismia cayennensis*, is a strong sprouter (Table 2) that has a well-developed root system with long, thick and unbranched roots (Pavlis & Jeník 2000) that store nutrients and allows stump and clonal resprouting. These traits likely make plants more dependent on and responsive to mycorrhizal symbiosis (Freitas 2005). Such below-ground traits may guarantee competitive advantages to *V. cayennensis* over other species under poor soil conditions (Freitas 2005). The interaction between below-ground plant traits (including mycorrhizal symbiosis) and land-use intensification merits further study. High dominance of *Vismia* species has previously been associated with abandoned pasturelands (Mesquita et al. 2001, 2015; Barlow et al. 2007), but here we show that intensive shifting cultivation can also promote *Vismia*-dominated successional pathways under conditions of poor soil quality.

The species assigned as indicators had different sprouting ability but also differed in other traits, such as maximum height and the capacity to cope with low soil quality (Fig. 2). Given that plants show a trade-off between investing in growth or in storage, species able to repeatedly resprout are usually slower-growing (Bond & Midgley 2001; Poorter et al. 2010). These slower-growing strong sprouters, such as *V. cayennensis*, *G. discolor*, *B. multijuga*, *C. spruceana* and *M. guianensis*, are out-competed by faster-growing species, such as *C. sciadophylla* and *J. copaia*, at low intensities of use but are favoured at higher frequency of disturbance. As a consequence of the selection for persistence strategies over regeneration strategies, along a gradient of land-use intensity the main processes structuring early successional communities will probably change from competition (for light) (Denslow & Guzman 2000) to survival (after disturbance).

Mechanisms underlying alternative successional pathways

Alternative successional pathways in the Amazon have been reported to continue to diverge during the first three decades of succession (Williamson et al. 2014, Longworth et al. 2014). Plant communities regenerating after clearcuts rapidly diverged, while on abandoned pastures lower rates of species accumulation sustained a similar plant

community through time (Longworth et al. 2014). At a very early stage of succession we already detected plant communities with different characteristics related to species composition, species diversity and regeneration strategies, indicating that the foundations of alternative pathways occur at the onset of succession.

Initial floristic composition is known to play an important role in determining species turnover in successional forests (Peña-Claros 2003). In 5-yr-old stands under *C. sciadophylla* and *J. copaia* canopies we observed higher α - and β -diversity (Fig. 3), which likely arose from legacies from the old-growth forest. These legacies will continue to play a role in further successional trajectories (Peterson & Carson 2008). With increasing land-use intensity, however, this diversity is reduced to a narrow set of species (Fig. 3b). When a diverse community is lacking at the onset of succession and regeneration depends mainly on resprouters, increasing diversity through time will depend on new incomers dispersed from surrounding sources. Given the low contribution of late successional species to seed rain in secondary forests (Holl et al. 2000; Benítez-Malvido et al. 2001; Cubiña & Aide 2001; Wieland et al. 2011), the fact that intensively used sites tend to be located in fragmented and deforested landscapes (Robiglio & Sinclair 2011) and the homogenization of plant communities in intensively used landscapes (Fig. 3b), species build-up is bound to be slow in these areas. This study supports the idea that filtering processes acting early in succession are primarily responsible for driving and sustaining alternative successional pathways.

Directions for future research and application

The lack of a good record of previous land use may be one of the reasons why chronosequence-based studies often deviate from long-term monitoring (Feldpausch et al. 2007; Walker et al. 2010b). Land-use history has been usually addressed in broad categories such as 'shifting agriculture' or 'pasture land', ignoring within-group variation in management practices and intensity. It is clear from our data that small differences in land-use intensity can be responsible for significant differences in species composition at early stages of succession. Therefore, we suggest that information on the number of swidden-fallow cycles or the number of burning events (Zarin et al. 2005) are good proxies for land-use intensity (Jakovac et al. 2015, and this study), and should be explicitly taken into account in secondary succession studies.

Our study identified a few early dominant tree species that are strongly associated with previous land use and could be used as indicators of land-use intensity in rapid field assessments or to validate land-use history. Our early plant communities are largely composed of pioneer species

with widespread occurrence in the Amazon region (Steininger 2000; Mesquita et al. 2001; Peña-Claros 2003; Barlow et al. 2007), implying that the patterns reported here are likely valid at much larger geographic scales. We propose that the dominance of secondary forests by the species *Cecropia sciadophylla*, *Jacaranda copaia*, *Croton palanostigma*, *Cassia spruceana* and *Vismia cayennensis* could be used as an indicator of increasing levels of previous land-use intensity in the Central Amazon region and beyond.

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Supporting Information

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

Appendix S1. Methodological procedures for selection of landscape size.

Appendix S2. Methods and additional results on sample completeness and species rarefaction curves.