

SPECIAL FEATURE

FOREST RESILIENCE, TIPPING POINTS AND GLOBAL CHANGE PROCESSES

Loss of secondary-forest resilience by land-use intensification in the AmazonCatarina C. Jakovac^{1,2*}, Marielos Peña-Claros¹, Thomas W. Kuyper³ and Frans Bongers¹

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Summary

1. Understanding how land-use intensification affects forest resilience is a key for elucidating the mechanisms underlying regeneration processes and for planning more sustainable land-use systems. Here, we evaluate how the intensification of a swidden cultivation system affects secondary-forest resilience in the Amazon.

2. Along a gradient of land-use intensity, we analysed the relative role of management intensity, soil properties and landscape configuration in determining the resilience of early secondary forests (SFs). We assessed resilience as the recovery level of forest structure and species diversity achieved by SFs 5 years after abandonment. We used as a reference the recovery level achieved by SFs subjected to the lowest intensity of use, given that these SFs are part of a dynamic system and may not develop to old-growth forests. Therefore, we interpreted a deviation from this reference level as a change in forest resilience.

3. The recovery of forest structure was determined by management intensity, while the recovery of species diversity was driven by landscape configuration. With increasing number of cycles and weeding frequency along with decreasing fallow period and patch area, SF basal area and canopy height decreased, regeneration shifted from a seed- to sprout-dependent strategy, and liana infestation on trees increased. With decreasing area covered by old-growth forest, species richness and Shannon diversity decreased.

4. Secondary-forest resilience decreased with land-use intensification, mainly mediated by the effect of management intensity upon regeneration strategies. Our findings demonstrate the – many times overlooked – importance of previous management intensity in determining the structure of SFs and highlight the importance of regeneration strategy for forest resilience.

5. *Synthesis.* Swidden cultivation supports people's livelihoods and transforms landscapes in the tropics. The sustainability of this system depends on ecosystem services provided by SFs that develop during the fallow period. Land-use intensification reduces the resilience of SFs and ultimately may drive the system towards an arrested succession state that holds a lower potential to deliver ecosystem services to the Amazonian people. Under an intensification scenario, the adaptation of management practices is needed to guarantee the resilience of swidden cultivation systems.

Key-words: Brazil, determinants of plant community diversity and structure, diversity, fire, landscape, legacies, resprout, secondary succession, soil, swidden agriculture

Introduction

Land-use and land-cover changes are the most important drivers of current global change. Understanding how resilient eco-

systems are to different types and intensities of land use is a key for elucidating the mechanisms underlying regeneration processes and for planning more sustainable land-use systems (Carpenter *et al.* 2001; Bengtsson *et al.* 2003). Ecological resilience is defined as the capacity of an ecosystem to absorb disturbances without changing its fundamental nature (Holling

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1973; Walker *et al.* 2004). Under this perspective, the understanding of the behaviour of a system concentrates not on the equilibrium state, but on the boundaries to the domain of attraction (Holling 1973). Accordingly, resilience can be assessed by the rate at which systems recover after disturbances (Pimm 1984), for which the limits of the system and the type of disturbance need to be previously defined (Carpenter *et al.* 2001). In tropical secondary forests (SFs), the resilience of plant communities to natural disturbances depends mainly on biological legacies (Bengtsson *et al.* 2003; Chazdon 2003), environmental conditions (Pickett *et al.* 1989) after disturbance and the sources for colonization in the remaining landscape matrix (Bengtsson *et al.* 2003; Hooper, Legendre & Condit 2004). During the first decades following natural disturbances, succession proceeds under high rates of increasing species richness, forest canopy height, density of stems and basal area of trees, and of decreasing canopy openness and abundance of herbs, shrubs and lianas (Finegan 1996). After high disturbance intensity, succession may deviate from this general pattern (Guariguata & Ostertag 2001; Mesquita *et al.* 2001), but it is not clear how the increasing intensity of anthropogenic disturbances will affect these factors, and consequently, the resilience of tropical SFs.

Secondary forests are gaining increasing importance in the tropics. In the Brazilian Amazon, 21% of the deforested areas until 2007 regrew to SFs, which are currently estimated to cover an area of ca. 150 000 km² (Almeida *et al.* 2010; INPE & EMBRAPA 2011). Located along the so-called arc of deforestation and the main rivers, most of these SFs are part of small-scale agricultural systems (Almeida *et al.* 2010). Swidden agriculture, also known as slash-and-burn or shifting cultivation, is the main agricultural system supporting people's livelihoods in the Amazon (Palm *et al.* 2005; Padoch 2010). It is based on a balance between disturbance and recovery and therefore constitutes an interesting model for evaluating the effects of anthropogenic disturbances on forest resilience. Swidden agriculture is a dynamic system in space and time, as forested areas are slashed and burned for crop cultivation and then left to fallow while new agricultural fields are opened (Nye & Greenland 1960; Coomes, Grimard & Burt 2000). The agricultural cycle length is variable within the Amazon region and may consist of short (1–3 years agriculture followed by 2–7 years fallow) or long cycles (>15 years fallow). Depending on farmers' decision, an area can also be left to regenerate towards old-growth forest. In the Amazon, within 1–2 years after abandonment, fallows already achieve a forest structure dominated by trees (Uhl *et al.* 1981), constituting early SFs. SFs deliver important ecosystem services that support the system, such as building-up nutrient stocks, suppressing weeds and pests (de Rouw 1995), protecting the soil from erosion and conserving water both on farm and downstream (Klemick 2011). SFs also provide a wide range of products to local people such as timber, firewood, fruits and fibres (Denevan & Padoch 1987; Chazdon & Coe 1999; Junqueira, Shepard & Clement 2010) and contribute to conserving habitat and species diversity in the landscape (Chazdon *et al.* 2009).

In the last decades, however, population pressure and socio-economic factors are driving agriculture towards intensification in an attempt to increase crop yield per unit of area and time (Coomes, Grimard & Burt 2000; Metzger 2002; Mertz *et al.* 2009; van Vliet *et al.* 2012). In areas with limited access to external inputs (i.e. herbicides), agricultural intensification is achieved by increasing the frequency of agricultural cycles with a predominance of short fallow periods (2–7 years) (Coomes, Grimard & Burt 2000; Schmook 2010). In the Amazon, fields that used to be cultivated for up to three swidden–fallow cycles now experience many more. With increasing number of cycles, the fallow duration also declines. Crop cultivation period has, however, remained constant (2-year cropping of manioc).

Increased land-use intensity modifies the landscape configuration by increasing the area covered by young SFs and cropping fields (Lawrence, Peart & Leighton 1998; Metzger 2002; Robiglio & Sinclair 2011). At the farm level, intensified management practices of recurrent cutting, burning and weeding may affect secondary succession through changes in the soil seed bank, seedlings and sprouts (Uhl 1987; Chazdon 2003). Recurrent burning of the standing biomass, crop harvesting and nutrient leaching may decrease biological, chemical and physical properties, as a consequence of land-use intensification (Arnason 1982; Palm, Swift & Woomer 1996; Lawrence *et al.* 2007; Runyan, D'Odorico & Lawrence 2012).

Studies in other tropical regions have reported decreases in biomass accumulation rate (Lawrence *et al.* 2010), shifts in species composition (Lawrence 2005a) and higher dominance by invasive species (Schneider & Fernando 2010) in SFs, as a consequence of increased number of swidden cycles. Nevertheless, the role of other management practices, soil quality and landscape configuration on SF resilience have hardly been jointly assessed (Lawrence 2004; Robiglio & Sinclair 2011). In the Amazon, studies on secondary succession have focused mostly on forest regrowth after clearcuts, pastures (Mesquita *et al.* 2001; Zarin *et al.* 2005) and after only one or few swidden–fallow cycles (Uhl *et al.* 1981; Peña-Claros 2003; Gehring, Denich & Vlek 2005; Lawrence *et al.* 2010). In this context, we aim to assess (i) the effects of the intensification of the swidden cultivation system on the resilience of SF in the Amazon and (ii) the relative importance of management intensity, soil properties and landscape configuration in this process (Fig. S1 in Supporting Information).

For this study, we did not use a chronosequence approach, but instead sampled same-aged SF along a broad gradient of land-use intensity. This approach allowed us to evaluate differences in recovery rate by directly comparing the recovery level achieved by same-aged SF. Given the high dynamics of swidden cultivation systems, SF in the landscape may not be left to develop to old-growth forests (Metzger 2002). Therefore, our reference for evaluating resilience is SFs that have been subjected to the minimum land-use intensity, that is, SFs growing in areas used for agriculture only once after slashing and burning old-growth forest and that were in a matrix of old-growth forests. Deviations from the recovery level achieved by these reference SFs would represent a change in the resilience of SFs. Given the importance of initial colonization in deter-

mining further successional pathways (Finegan 1996; Guariguata & Ostertag 2001) and the increasing extent of young SFs in agricultural landscapes (Metzger 2002; van Breugel *et al.* 2013), we focused on the first 5 years of forest succession.

We hypothesized that land-use intensification leads to a decrease in the resilience of SFs through changes in management intensity, soil quality and landscape configuration (Fig. S1). Specifically, we hypothesized that increasing management intensity (e.g. increased frequency of cycles and weeding; reduced fallow period) along with a decrease in the extent of old-growth forests in the landscape will lead to a decrease in species richness and diversity, and an increase in the relative abundance of lianas and resprouting trees in the community (Uhl *et al.* 1981; Lawrence 2004; Lawrence *et al.* 2010). Decreased soil fertility will lead to a decrease in the density of individuals, canopy height and an increase in canopy openness (Lawrence *et al.* 2007). By evaluating at the same time how these three groups of factors affect the recovery of key components of secondary succession, we aim to elucidate some of the mechanisms underlying secondary-forest resilience loss.

Materials and methods

STUDY SITE

The study was carried out in the municipalities of Tefé and Alvarães located in the region of the middle Amazonas River, in the Central Amazon, Brazil (Fig. S2 in Supporting Information). We sampled 38 early secondary forests (SFs) in five communities, named Agrovila (10 SFs), Nogueira (11 SFs), Vila São (six SFs), São Francisco (six SFs) and São Sebastião (five SFs). Villages were located along the black water Tefé River and tributaries (Fig. S2) and were at least 3 km and at maximum 66 km distant from each other. The main agricultural activity in the villages is the cultivation of bitter manioc and the production of manioc flour, which is the staple food of Amazonian people. Manioc flour is produced for self-consumption, with the surplus being commercialized in the local market (Tefé, around 60 000 inhabitants) and shipped to the bigger cities. Both manioc cultivation and flour production are based on traditional practices and on family and collective work. Manioc is cultivated using swidden agriculture by local smallholder farmers, in small fields of 1–3 ha. In the study site, agriculture is done in non-flooded areas (*terra firme*) over poor soils classified as oxisols and ultisols.

During the last 30 years, human population in Tefé and surrounding towns has increased. This resulted in a higher demand for manioc flour, which together with other socio-economic drivers led to intensification of the traditional swidden cultivation. More agricultural cycles are being done in the same area, and consequently, fallowing period has decreased. However, in the study area, the cropping period still lasts for 2 years, with only one manioc harvest per cycle.

DATA COLLECTION AND ANALYSES

We sampled 38 SFs distributed along land-use intensity gradients in each village. We sampled only SFs with an average age after harvesting of the last cropping cycle (current fallow age) of 5 ± 0.1 (SE) years. We chose to sample only SFs within one age class for several reasons. First, we were interested in investigating the other possible factors affecting SFs without considering the effect of age. Secondly,

with this sampling design, we could directly invoke recovery rates without relying on estimated growth rate curves. Finally, we selected this specific age class because it was the most abundant in the villages and was the oldest age available in all villages. For each SF, we evaluated the management practices applied, vegetation structure and diversity, soil properties and landscape configuration and recorded its geographical location.

We selected SFs based on information provided by landowners on the land-use history of the sites. We assessed this information by interviewing landowners and their families. The first approach was an open interview where they were asked to describe how they cultivate their fields and what are the management practices used. After that, we walked to the SFs and asked how management was done in that specific field. From their description and from direct questionnaires, we extracted information about (i) the current fallow age, (ii) the number of cycles that have taken place since old-growth forest was slashed, (iii) the age of the former fallow that was slashed before the last cropping cycle, and (iv) the number of times the previous cropping field was weeded. Information was cross-checked by asking questions in different ways and at different moments as well as to other members of the family.

In each selected SF, we sampled trees, shrubs, palms and lianas using transects allocated at the centre of the SF patch. In each transect, we sampled every woody individual (trees, palms and shrubs) with diameter at breast height (d.b.h.) >5 cm in 10×50 m (canopy size class), individuals with $1 \text{ cm} < \text{d.b.h.} < 5 \text{ cm}$ in 5×50 m (understorey size class) and individuals with $\text{d.b.h.} < 1 \text{ cm}$ and $\geq 1 \text{ m}$ height in 3×50 m (sapling size class). For canopy and understorey size classes, we measured d.b.h. and estimated height, while for the sapling size class, we only measured height. We identified all sampled individuals to species or morphospecies (but floristic composition will not be shown here). We estimated stand canopy openness using a convex densitometer (Lemon 1956), taking six measurements per transect. We took measurements every 10 m, along the central line of the 10×50 m transect, starting from 0 m. At each measurement point, we took four measurements, which were then averaged. Canopy openness was represented by the average of the measurements taken at each measurement point along each transect.

For each tree, palm and shrub, we checked whether it was a resprout or not and classified its crown position and its degree of liana infestation. We considered an individual as a resprout when the tree was regenerating from a stump or when it was connected by roots at the soil surface. Stems from the same species that were ≤ 50 cm apart were also considered as belonging to the same individual. By excavating in some cases, we verified that these stems (ramets) indeed belonged to the same individual (genet). Consequently, in further calculations of stand structure descriptors, we distinguished between density of individuals (genets) and density of stems (ramets). Each individual was assigned to a crown position as (i) with no direct light reaching the crown, (ii) some side light, (iii) some overhead light, (iv) full overhead light, and (v) emergent crown (Dawkins & Field 1978) and to the presence or not of lianas in the crown and/or trunk of the trees (presence/absence).

At each SF, we collected samples for soil chemical and physical analysis. In each plot, we collected 5 samples from the first 20 cm using a bucket auger, which were combined to one composite sample. Samples were air-dried, stored in plastic bags and taken to the EMBRAPA soil laboratory. The following parameters were assessed following published protocol (EMBRAPA 2011): soil organic carbon, total N, available P, K, Ca, Mg, Fe, pH and Al, and the percentage of the different particle sizes [sand (0.05–2.00 mm), silt (0.002–0.05 mm) and clay (<0.002 mm)].

To describe the landscape configuration, we quantified the linear distance to the nearest old-growth forest and the area covered by old-growth forest in a 500 m radius (78.5 ha) around each SF. The geographical location of each SF was recorded in the field using a GPS and then plotted on the land-use cover classification map provided by the Program for the Estimation of Deforestation in the Brazilian Amazon-PRODES for 2011 (INPE 2011). Based on ground truthing of the limits of old-growth forest and land use reported by the landowners, we improved the PRODES classification map by redefining the old-growth forest edges. Using GIS tools, we located the centroid of each SF and then calculated its linear distance to the nearest old-growth forest edge and the area covered by old-growth forest within a 500 m radius around the SF centroid. Calculations were done in ARCGIS 10.1 (ESRI 2012).

STATISTICAL ANALYSES

To define a gradient of management intensity, we selected descriptors that have been related to land-use intensification in the literature (Lawrence 2004; Mertz *et al.* 2009; van Vliet *et al.* 2012) and by farmers from the study site. Among all the information we acquired from the landowners, we selected the following four descriptors of management and summarized them by performing a principal component analysis – PCA: number of swidden–fallow cycles (1–10 cycles), age of the previous fallow (2–7 years; when the previous vegetation was an old-growth forest, we attributed an age of 100 years), number of times the former manioc field was weeded (1–4 weeding) and the area of the current SF patch (Table 1). Cropping period (2 years) and current SF age (5 years) were invariant and therefore not included in the PCA. Multivariate analyses were done in Canoco 5.0 (Ter Braak & Smilauer 2012). We applied Horn's parallel analysis (PA) with 120

iterations (30 iterations per variable) to evaluate the significance of the components to be retained in the PCA. Threshold used for retaining a component was an adjusted eigenvalue > 1. PA was processed using paran package in R 3.0.2 (R Development Core Team 2013).

For each SF, we calculated the following variables as descriptors of vegetation structure: stand total basal area ($\text{m}^2 \text{ha}^{-1}$), density of genets (indv ha^{-1}) and ramets (stems ha^{-1}), canopy height (m) (defined as the mean height of trees with crown position ≥ 4), canopy openness (%), percentage of resprouts (percentage of resprouting individuals) and liana infestation (defined as the percentage of trees with some degree of liana infestation). We represented diversity of the secondary-forest stands by the following descriptors: species richness, rarefied species richness and Shannon and inverse Simpson ($1/D$, where $D = 1 - \sum p_i^2$) diversity indexes. Stand species richness was rarefied to 150 individuals, using all individuals sampled in the three size classes described earlier. Calculations for diversity were processed with vegan package in R 3.0.2 (R Development Core Team 2013).

Soil variables were summarized through a PCA, in which we included the 12 variables indicated above. We did not include derived variables such as cation exchange capacity – CEC and aluminium saturation – as those were highly correlated with the individual variables. All variables included in the PCAs were previously centred and standardized before analysis. We also applied a PA analysis with 360 iterations (30 iterations per variable included) to decide which component of the PCA to be retained. Threshold used for retaining a component was an adjusted eigenvalue > 1.

To evaluate the effect of management intensity, soil properties and landscape configuration on SF structure and diversity parameters, we used mixed-effects models. We included as fixed factors the scores of

Table 1. General characteristics of 38 early secondary-forest patches in central Amazon, Brazil. Mean, standard deviation (SD), and minimum and maximum values for each explanatory variable are included. For management intensity and soil properties, the loading on the retained axes of each PCA is provided in italic (see also Fig. 1). Significance levels are based on a Pearson correlation between individual variables and PCA axes

	Mean	SD	Min	Max	PCA	
					Axis 1	Axis 2
Management intensity						
Number of swidden–fallow cycles	3.8	2.2	1.0	10.0	0.78**	
Mean number of weedings	2.4	0.8	1.0	3.5	0.86**	
Previous fallow age	19.3	35.0	2.0	100.0	–0.82**	
Secondary-forest patch area	1.1	0.8	0.3	3.7	–0.73**	
<i>Explained variation by PCA (%)</i>					<i>64.0</i>	
Soil quality						
Percentage of clay (%)	17.8	7.6	7.0	35.0	–0.73**	0.04
Percentage of silt (%)	33.4	10.0	15.0	50.0	–0.68**	0.32
Percentage of sand (%)	48.9	13.7	31.0	77.0	0.89**	–0.23
pH (H ₂ O)	3.7	0.3	3.4	4.3	–0.01	0.84**
Al (cmol dm ^{–3})	4.4	1.2	2.2	7.4	–0.87**	–0.01
C (g kg ^{–1})	17.4	5.3	9.6	28.5	–0.86**	–0.27
Ca (cmol dm ^{–3})	0.1	0.0	0.0	0.1	–0.62**	–0.28
K (cmol dm ^{–3})	0.1	0.0	0.0	0.1	–0.72**	0.03
Mg (cmol dm ^{–3})	0.2	0.1	0.1	0.3	–0.52*	0.21
N (g kg ^{–1})	1.3	0.4	0.8	2.2	–0.84**	–0.43*
Fe (mg dm ^{–3})	279.0	90.7	134.0	475.0	0.04	0.76**
P (cmol dm ^{–3})	0.1	0.0	0.0	0.1	0.28	–0.73**
<i>Explained variation by PCA (%)</i>					<i>43.8</i>	<i>19.7</i>
Landscape configuration						
Linear distance to the forest (m)	507	444	0	1753	–	–
Area of forest within 500 m radius (ha)	10.9	17.8	0	78.5	–	–

* $P \leq 0.05$, ** $P \leq 0.01$.

the first axis of the land-use intensity PCA, the first and second axes of the soil PCA, the area covered by old-growth forest and the linear distance to the old-growth forest. Village was included as a random factor. All variables were centred and standardized before analysis. We performed model selection by stepwise removal of the least significant fixed factors, applying the maximum likelihood method of parameter estimation until we got to the final model with the lowest Akaike information criterion (AIC) value. In general, only significant factors were retained in the final model, but in cases when a non-significant factor considerably increased the fit of the model, it was retained as well (Zuur *et al.* 2009). We then re-fitted the final model with the restricted maximum likelihood method (REML) to extract the unbiased estimated parameters (Zuur *et al.* 2009). We present here only the results of the REML-estimated final models. The linear distance to the old-growth forest was not included in the final model as previous analyses showed that it did not have an effect on any tested response variable. All variables represented by percentages (% respout, % liana infestation and % canopy openness) were transformed by the arcsine of the square root of the percentage prior to statistical analysis. The variables basal area, density of genets, density of ramets, species richness, and Shannon and inverse Simpson diversity indexes were all ln-transformed.

We also correlated all individual variables using Pearson correlations (Table S2, Supporting Information). We applied an adjusted Bonferroni correction for multiple comparisons, setting the significance level for these correlations at 0.0018. Statistical analyses were done with nlme package in R 3.0.2 (R Development Core Team 2013).

Results

SECONDARY FORESTS AND THE DESCRIPTORS OF LAND-USE INTENSIFICATION

The 38 sampled SFs had a mean age after abandonment of 5.0 ± 0.1 (SE), were subjected to different management intensities (Fig. 1a) and were located at different distances from the old-growth forest. The closest SF was located immediately

adjacent to the old-growth forest and had a maximum of 78 ha of forest surrounding it (99% within a 500 m radius), and the furthest SF was 1.7 km apart from the forest edge and had no old-growth forest within that radius (Table 1).

The first two axes of the management intensity PCA explained 80% of the variation in the data (Fig. 1). The first axis was significantly correlated with all descriptors of management (Table 1), weeding, age of previous fallow, number of swidden-fallow cycles, and area of the SF patch, and explained 64% of the variation. The second axis explained 16% of the variation and was significantly correlated with the area of the current SF patch and the number of cycles. The Horn's parallel analysis indicated that only the first axis should be retained (adjusted eigenvalue = 2.66); therefore, in further analyses, we only used this axis to represent management intensity. We will refer to it as the management intensity axis.

Soils had in general low fertility, low pH, low P availability and high aluminium content (Table 1). The first two axes of the soil PCA explained 64% of the variation in the soil data. The first axis explained 44% of the variation and was negatively correlated with clay and silt, Al, soil organic carbon and nutrients (Fig. 1b). The second axis explained 20% of the variation and was positively correlated with pH and Fe and negatively to P (Table 1). The Horn's parallel analysis indicated that the first two axes should be retained (adjusted eigenvalues = 4.17 and 1.62 for the first and second axes, respectively). Hereafter, we will refer to the first PCA axis as the soil texture axis and to the second axis as the soil acidity axis. Soil texture and soil acidity axes were not significantly correlated with the management intensity axis nor to the area covered by old-growth forest (see Table S1 in Supporting Information). The area covered by old-growth forest was significantly correlated with the management intensity axis (Pearson correlation, $R = -0.65$, $P < 0.001$, $n = 38$) (Table S1).

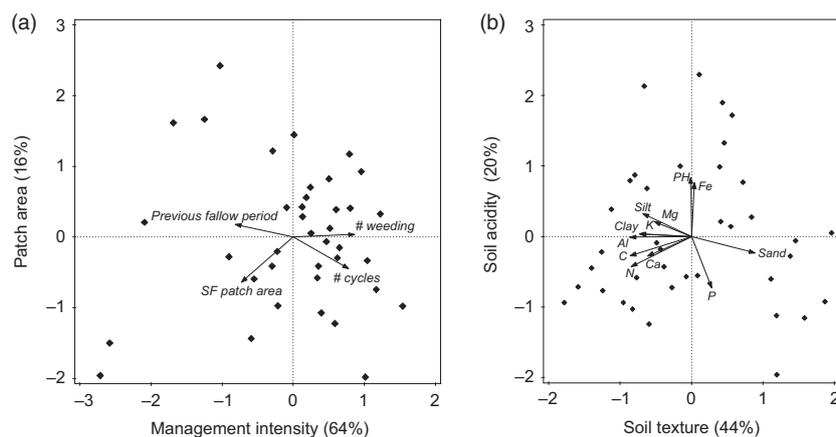


Fig. 1. Management intensity and soil quality descriptors of early secondary forests (SFs) in central Amazon, Brazil. Principal component analyses (PCA) of the 38 sampled SFs near Tefé, central Amazon, Brazil, using (a) previous fallow period, number of weeding events (# weeding), number of previous swidden cycles (# cycles), current secondary-forest patch area (SF patch area); and (b) soil texture and chemical characteristics (Table 1). Percentage of variation explained by each axis is provided. Dots represent the 38 sampled SFs. Arrows represent each variable used for ordering the plots along the axes. The lower the angle between the arrow and a given axis, the stronger the influence of that variable in the ordination of the plots along that given axis.

EFFECTS OF LAND-USE INTENSIFICATION ON FOREST RESILIENCE

The recovery of SF structure was significantly related to management intensity, soil texture and soil acidity, with no significant effect of the area covered by old-growth forest.

For five out of seven forest structure variables, management intensity was the only significant factor (Table 3): percentage of resprouting individuals, liana infestation and density of ramets increased with management intensity, while stand basal area and canopy height decreased (Fig. 2). By increasing management intensity, SFs increasingly deviated from the recovery level achieved by same-aged SFs subjected to the lowest intensity of use (Fig. 2). Moving one unit on the management intensity axis (Fig. 2), basal area decreased $2.9 \text{ m}^2 \text{ ha}^{-1}$, canopy height decreased 1.4 m, stems density increased in 2959 stems ha^{-1} , resprouters increased in 15% and liana infestation increased in 8% (Table S3 in Supporting Information, Figs 2 and 3). Only two forest structure variables were affected by soil characteristics, at a marginal significance level (Table 3). Density of genets was negatively related to the soil texture axis, increasing with clay content (Table 3 and Fig. 1b). Canopy openness was positively related to soil acidity axis, increasing with soil pH (Table 3 and Fig. 1b).

The species richness and diversity indices achieved by SFs 5 years after abandonment significantly increased with area of surrounding old-growth forest (Table 3). Within 5 years of succession, SFs immediately surrounded by old-growth forest achieved 30% more species (ca. 25 species, based on rarefied richness) than SFs without surrounding forest (Fig. 3, Table S3). Inverse Simpson diversity also slightly increased with management intensity (Table 3). Species richness, rarefied richness and Shannon diversity were also affected by soil

acidity axis, decreasing with soil pH (Fig. 3). The effect size of soil on the recovery level achieved by SFs, in terms of structure and diversity, was always lower than the effects of management intensity and area of surrounding forest (Fig. 4).

Discussion

In this study, we assessed the effect of intensification of swidden cultivation on the resilience of SFs in central Amazon. We found a decrease in forest resilience with increasing land-use intensification. The recovery of forest structure was mainly determined by management intensity, and diversity recovery was driven by landscape configuration. Soil properties had a limited effect on forest structure and diversity (Fig. 4).

THE EFFECT OF MANAGEMENT INTENSITY ON FOREST RESILIENCE

Intensified management practices lead to a steep decrease in the forest structure level achieved by SFs 5 years after abandonment. Our findings demonstrate the – many times overlooked – importance of management practices in determining the structure of SFs and indicate a strong link between regeneration strategies and forest resilience. The proportion of resprouts in the regenerating community strongly increased as an effect of intensified management practices (Table 3). This proportion increases both because resprouters are favoured and the seed bank is reduced (Uhl 1987). Recurring cutting and burning of SF trees probably select for species that have below-ground nutrient storage, which is protected from fire and allows for recovery after each agricultural cycle (Bond &

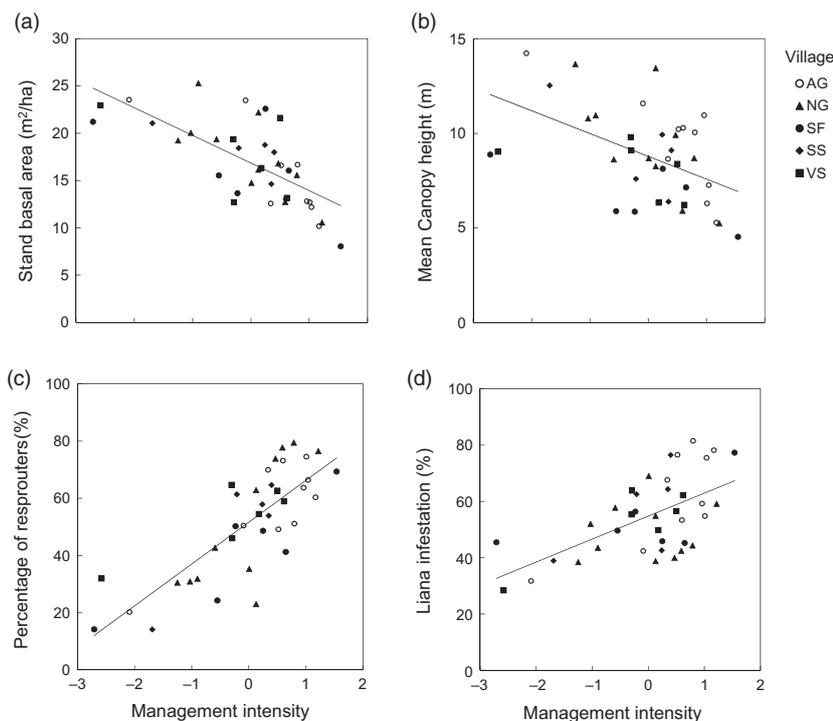


Fig. 2. The effect of management intensity on structural parameters in secondary forests (SFs) in central Amazon, Brazil. (a) Stand basal area, (b) mean canopy height, (c) percentage of resprouters and (d) percentage of liana infestation on trees as a function of management intensity. Management intensity here is represented by the scores extracted from the first axis of the management intensity PCA (Fig. 1a). Higher scores represent an increase in the number of cycles and weeding frequency, a decrease in the length of the previous fallow period and, to a lower extent, the area of the secondary-forest patch (Fig. 1a). Symbols indicate the SFs belonging to the different villages: Agrovila (AG), Nogueira (NG), São Francisco (SF), São Sebastião (SS) and Vila Sião (VS).

Fig. 3. Effect of area of surrounding forest and soil acidity on species richness of secondary forests in central Amazon, Brazil. (a) Relationships between rarefied richness with 150 individuals (rarefied species richness) and the area of surrounding old-growth forest within 500 m radius of each secondary-forest patch (area of surrounding forest); (b) residuals of the linear mixed-effects model of rarefied species richness against area of surrounding forest as a function of the second axis of soil PCA (soil acidity, Fig. 1b).

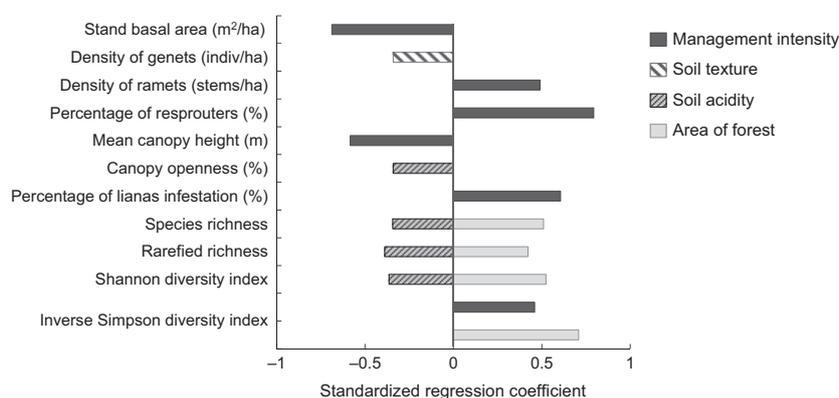
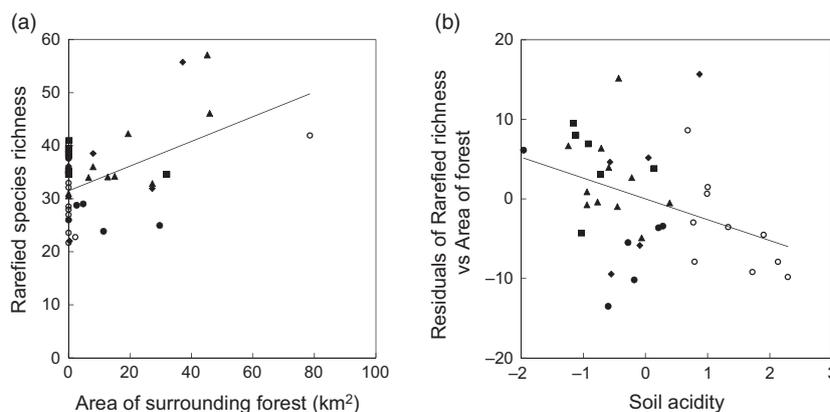


Fig. 4. Effect size of the explanatory variables on vegetation structure and species diversity of early secondary forests in central Amazon, Brazil. Standardized regression coefficients estimated by linear mixed-effects models of vegetation structure and species diversity as a function of management intensity axis (Fig. 1a), soil texture axis, soil acidity axis (Fig. 1b) and area of surrounding old-growth forest within 500 m radius of each secondary-forest patch (area of forest). The standardized regression coefficients can directly be compared among each other; the higher the value, the stronger the relationship observed. The sign of the coefficient represents the direction of the relationship. Only significant effects are included (see Table S3 for more information).

Midgley 2001). Weeding, mostly done by cutting and pulling out weak-rooted seedlings, may also favour strong-rooted sprouters. Weeding and recurrent burning along with seed predation, which is usually high in open areas and in early successional forests (Peña-Claros & De Boo 2002), may contribute to depleting the seed bank (Uhl *et al.* 1981).

In fire-prone and frequently disturbed systems, only species that are able to sprout after losing their above-ground biomass several times are able to survive (Bond & Midgley 2001). These strong sprouters have high capacity of below-ground storage and generally sprout several stems, which trades off against allocation to growth (Kruger, Midgley & Cowling 2003; Poorter *et al.* 2010). Consequently, stands dominated by these strong sprouters showed higher density of ramets (even at constant density of individuals), lower basal area and shorter canopy (Fig. 2). Therefore, the shift we observed from a seed-dependent towards a sprout-dependent regeneration mechanism with increasing management intensity (Fig. 2) determines the structure of SF stands. Lawrence (2005b) has already suggested a relation between the decrease in above-ground biomass and the increased presence of resprouting species. Our study corroborates this hypothesis. The predominance of

sprouters at early stages of succession may indicate reduced species turnover, as sprouters favour self-replacement (Bond & Midgley 2001), and as the increase in species richness and diversity throughout secondary succession strongly depends on seed dispersal from forests nearby. Therefore, under a land-use intensification scenario, sprouters may dominate the community in the long term (also shown by Norden *et al.* 2011).

Contrary to our hypotheses, we did not detect a strong effect of management intensity on the recovery of species richness and diversity. Only diversity estimated by inverse Simpson index slightly increased with management intensity (Fig. 4). This diversity index is more sensitive to changes in common species, and therefore, its relation to management intensity might follow the increasing dominance of sprouting species. Sprouting species from the genus *Vismia* (e.g. *V. cayannensis*, *V. gracilis*) dominated the intensively used SFs in our study site (*data not shown*). *Vismia* spp. also dominate post-pasture SFs in central Amazon (Mesquita *et al.* 2001), forming large patches of clonal individuals (R. C. G. Mesquita, unpubl. data). Although we did not find strong evidence for changing species number with management intensity, species composition is very likely to be changing.

Increasing management intensity also leads to an increase in liana infestation on trees (Table 3). Liana and other non-woody life forms are the first to colonize open areas immediately after natural disturbances and gradually disappear under the shade of trees, which form a continuous canopy in <3 years (Finegan 1996). Under low intensity of use, 5-year SFs had around 30% of trees supporting lianas, but with increasing management intensity, this proportion reached up to 80% (Fig. 2d). This increase indicates a longer time persistence of lianas in the system and therefore a lower rate of succession. The increased liana infestation also represents an important constraint to the development of SFs, as lianas compete both above-ground for light and below-ground for water and nutrients (Schnitzer, Kuzee & Bongers 2005; Schnitzer & Carson 2010). Therefore, extreme liana infestation levels, such as those we observed in the more intensively managed fields (Fig. 2d), may hinder further succession.

THE EFFECTS OF SOIL PROPERTIES ON FOREST RESILIENCE

Soil properties did not explain changes in the recovery level achieved by same-aged SFs in terms of forest structure and diversity (Table 3). This conclusion seems in contrast to studies that showed a decrease in soil quality with land-use intensification (Lawrence *et al.* 2007; Runyan, D'Odorico & Lawrence 2012) and studies that related soil fertility decline to decreased forest recovery rate in swidden cultivation (Moran *et al.* 2000; Lawrence *et al.* 2007).

Significant correlations of number of swidden–fallow cycles with clay ($R = -0.44$, $P = 0.006$; Table S2) and pH ($R = 0.48$, $P = 0.003$; Table S2) suggest effects of land-use intensification on soil properties (Table S2). Recurrent fires can change soil texture by increasing sand and reducing clay content (Terefe *et al.* 2008) through leaching and erosion (Certini 2005). Nevertheless, the large variability in soil texture and associated soil fertility among our samples probably overrode the effect of land-use intensity on soil texture axis and, consequently, on SF resilience. The increase in soil pH with number of cycles (Table S2) might also be a consequence of burning that recurrently adds ash to the soil surface (Nye & Greenland 1960; Certini 2005). Additionally, the negative correlation between available P and pH ($R = -0.60$, $P < 0.001$, Table S1), where in this pH range, one would expect both to be positively correlated, suggests losses of P with increased burning frequency. Therefore, the significant effects of the soil acidity axis on canopy openness, species richness and Shannon diversity index are probably indicative of increased number of cycles and recurrent burnings (Fig. 4).

A progressive loss of phosphorus availability with increasing number of swidden cycles has been related to the decreased rate of fallow regrowth (Runyan, D'Odorico & Lawrence 2012). However, those studies reported P levels at least three times higher than what this (Table 2) and other studies in the Amazon have found (Laurence *et al.* 1999; Moran *et al.* 2000). Even though we had a broad gradient of land-use intensity, P availability ranged very little

Table 2. Vegetation structure and species diversity of 38 early secondary forests in central Amazon, Brazil. Data provided are mean, standard deviation (SD) and range

	Mean	SD	Min	Max
Structure				
Stand basal area (m ² ha ⁻¹)	16.9	4.3	8.1	25.3
Density of genets (indiv ha ⁻¹)	11 748	3868	6260	27 233
Density of ramets (stems ha ⁻¹)	16 861	6103	8340	31 027
Percentage of resprouters (%)	51.6	18.7	14.1	79.4
Mean canopy height (m)	8.8	2.4	4.5	14.2
Canopy openness (%)	15.7	6	6	31
Percentage of lianas infestation (%)	54.8	13.8	28.3	81.5
Diversity				
Richness (number of sampled species)	41.7	10.4	26	70
Richness (rarefied to 150 individuals)	34.0	8.2	21.7	57.1
Shannon diversity index	2.8	0.4	1.8	3.7
Inverse Simpson diversity index	11.2	5.8	2.7	25.8

(Table 1) and was not related to forest structure (Table S2). In swidden systems over weathered poor acid soils, the biomass that is burned (from an old-growth forest or from a SF) is what probably supports the crop yield and fallow regrowth (Palm, Swift & Woomer 1996; Silva-Forsberg & Fearnside 1997). Our results showing that management intensity but not soil properties affected SF recovery corroborate this idea.

THE EFFECT OF LANDSCAPE CONFIGURATION ON FOREST RESILIENCE

Landscape configuration had an important effect on the recovery of species richness and diversity. As we hypothesized, the larger the area of old-growth forest surrounding the patches, the faster species richness and diversity increase in SFs (Table 3, Table S3 and Fig. 3). This is probably due to a reduced propagule dispersal probability with increasing distance from the source (Helmer 2000; Cubiña & Aide 2001). Not only old-growth forests but also developed SFs may act as important sources of diversity. SF patches located closer to the old-growth forest were also surrounded by less intensively used SFs (Table S2), increasing the species richness of the matrix and thereby strengthening the effects on diversity. It is impressive that such effects could be detected in landscapes still largely covered by old-growth forests, where agricultural areas cover a radius of only ca. 2 km from the villages households and are surrounded by continuous old-growth forest extending for thousands of kilometres inland (Fig. S2). Given that species accumulate through time in successional forests

Table 3. Effects of management intensity, soil properties and landscape configuration on early secondary forests in central Amazon, Brazil. Results from linear mixed-effects analyses performed on vegetation structure and species diversity of secondary forests as a function of management intensity PCA axis (Manag. intensity), soil PCA first axis (Soil texture), soil PCA second axis (Soil acidity) and area of surrounding old-growth forest in a 500 m radius (Area of forest). *t* and *P*-values of each predictor and the degrees of freedom (d.f.) of the final model are provided

Response variables	d.f.	Manag. intensity		Soil texture		Soil acidity		Area of forest	
		<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Structure									
Stand basal area (m ² ha ⁻¹)	32	5.67	< 0.001						
Density of genets (indiv ha ⁻¹)	32			-2.06	0.047				
Density of ramets (stems ha ⁻¹)	32	-4.17	< 0.001						
Percentage of resprouters (%)	32	-7.82	< 0.001						
Mean canopy height (m)	32	4.60	< 0.001						
Canopy openness (%)	32					-2.19	0.04		
Percentage of lianas infestation (%)	32	-4.58	< 0.001						
Diversity									
Richness (number of sampled species)	31					-2.11	0.04	4.19	< 0.001
Richness (rarefied to 150 individuals)	31					-2.27	0.03	3.25	< 0.001
Shannon diversity index	30	-1.73	NS			-2.29	0.03	2.72	0.01
Inverse Simpson diversity index	31	-2.51	0.02					3.82	< 0.001

(Finegan 1996), we can expect species richness and diversity to increasingly deviate in SFs under different landscape configuration.

TOWARDS ALTERNATIVE SUCCESSIONAL TRAJECTORIES

The changes in SF structure, diversity and regeneration mechanisms identified as a consequence of land-use intensification (Figs 2 and 3) may suggest that this system is moving towards an alternative successional trajectory, as already suggested for other more intensive land uses (e.g. cattle ranching; Mesquita *et al.* 2001; Hooper, Legendre & Condit 2004; Williamson *et al.* 2014). Our results clearly show that with land-use intensification, vegetation structure increasingly deviates from the natural successional process (represented by the least used sites) (Fig. S3 in Supporting Information), showing ever lower recovery rates (Figs 2 and 3). Under extreme conditions, it may move towards an alternative trajectory, and the system will persist as such if positive feedbacks preclude it to return to its former state (Scheffer *et al.* 2012). In our system, potential positive feedbacks are the increased dominance of sprouters and liana infestation and an expected decrease in the extent of old-growth forests in intensified landscapes. Such feedbacks may preclude these SFs to approach a successional pathway achieved under less intensified conditions. Although our methodology did not allow us to evaluate how those SFs will develop over time, chronosequence and monitoring studies in the central Amazon found low recovery rates and seedling growth in SFs regrowing after the abandonment of pasturelands managed by prescribed burning (Norden *et al.* 2011; Jakovac *et al.* 2014; Williamson *et al.* 2014). In such systems, sprouting species have dominated for more than 25 years, and so far, there is no evidence of convergence to

the original successional trajectory (Williamson *et al.* 1998; Mesquita *et al.* 2001; Longworth *et al.* in press). Therefore, it is likely that strong intensification of swidden cultivation will also push SFs into an arrested successional state, comparable with those found in abandoned pastures.

IMPLICATIONS

The current intensification of swidden cultivation systems may have important socio-economic consequences. One such consequence is the reduction of crop productivity (Arnason 1982; Silva-Forsberg & Fearnside 1997) as a result of reduced above-ground biomass of fallows and higher labour demand for weeding (de Rouw 1995), directly related to the dominance of resprouters. Land-use intensification may also reduce the potential use of SFs as sources of provisioning services (e.g. timber, fire-wood, fruits) for the local populations and threaten the conservation value of these agricultural landscapes (Chazdon *et al.* 2009; Padoch 2010). Under a scenario of increasing pressure for land-use intensification, management practices must be adapted. Unassisted regeneration will not guarantee the sustainability of the system; therefore, SFs should be more intensively managed to improve recovery rate and/or fallow quality. Fostering economic exploitation of secondary-forest products could decrease agricultural pressure and allow for longer fallow periods as income could be generated from the fallow and crop periods. Nevertheless, this might not be an option under high land pressure and high crop demand. In this case, planting or favouring fast-growing species and excluding strong sprouters could improve fallow recovery rates. To guarantee the resilience of the system as a whole under an intensification scenario, adaptive management practices must be fostered both by local farmers as well as by institutions.

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Data accessibility

The data from this study will be archived at the EASY online archiving system of the Dutch Data Archiving and Networked Services (DANS): <https://easy.dans.knaw.nl/ui/home>.

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Supporting Information

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

Table S1. Pearson correlation among predictors included in the linear mixed-effects analysis.

Table S2. Pearson correlation among all individual variables included in the analyses.

Table S3. Non-standardized effect size of the explanatory variables on vegetation structure and species diversity of early secondary forests in central Amazon, Brazil.

Figure S1. Conceptual framework on how land-use intensification affects secondary-forest resilience.

Figure S2. Map of the study area.

Figure S3. Diagram of the effects of land-use intensity on the structure of secondary forests.