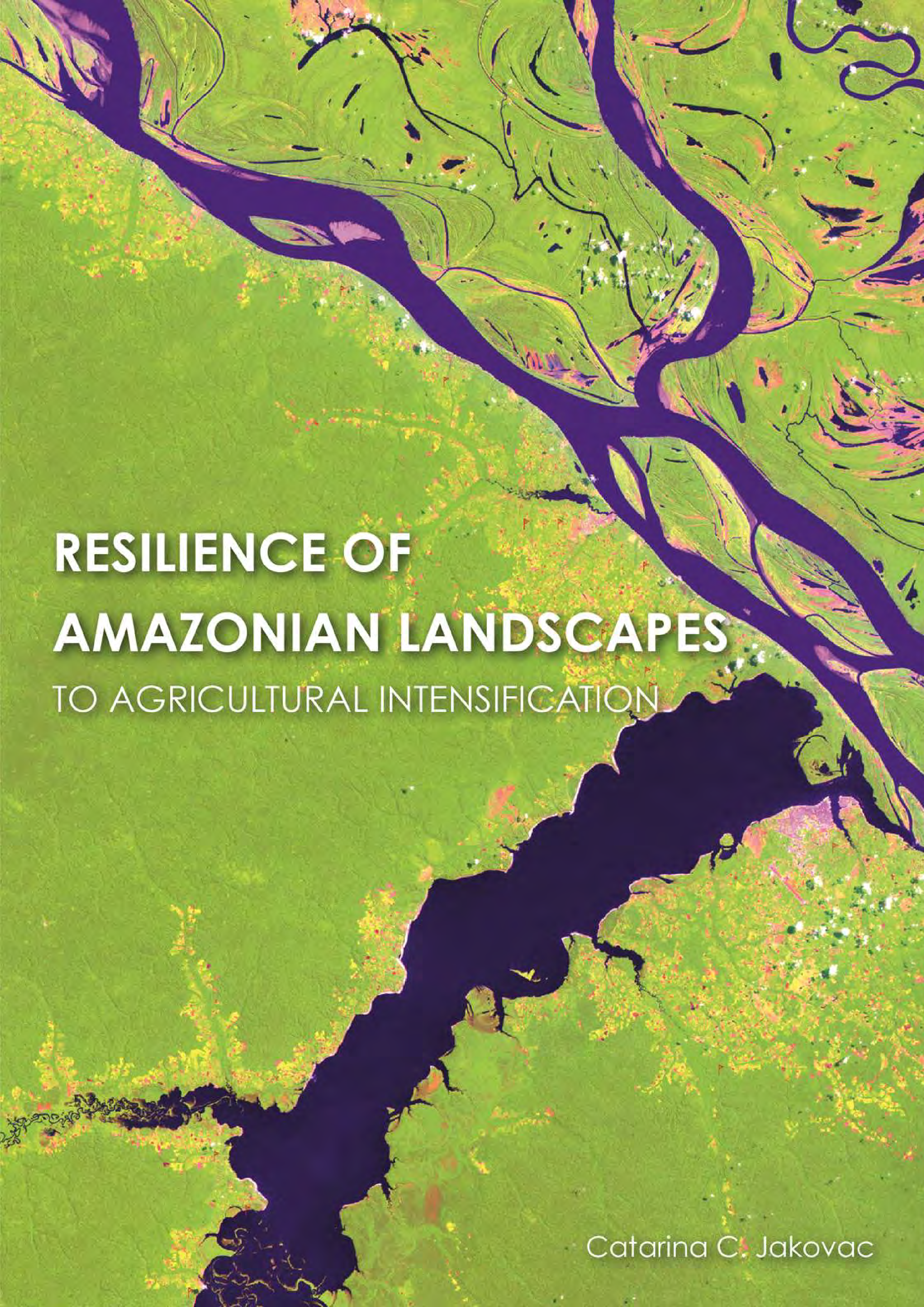

RESILIENCE OF AMAZONIAN LANDSCAPES

TO AGRICULTURAL INTENSIFICATION

Catarina C. Jakovac

Resilience of Amazonian landscapes to agricultural intensification

Catarina C. Jakovac

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This research was conducted under the auspices of the C. T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC).

Resilience of Amazonian landscapes to agricultural intensification

Catarina C. Jakovac

Thesis
submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University
by the authority of the Rector Magnificus
Prof. Dr A.P.J. Mol,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Wednesday 30 September 2015
at 4 p.m. in the Aula.

Catarina C. Jakovac
Resilience of Amazonian landscapes to agricultural intensification
176 pages.

PhD thesis, Wageningen University, Wageningen, NL (2015)
With references and summary in English

ISBN 978-94-6257-443-4

To Paulo and Angela

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General introduction

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HUMAN-TRANSFORMED LANDSCAPES IN THE TROPICS

In a world increasingly modified by human activities, finding a balance between agricultural production and nature conservation is a growing challenge. Development towards specialization and intensification of agricultural production has guaranteed food supply to a growing human population, however has also resulted in adverse side effects on biodiversity and rural societies (van Vliet et al. 2012, Grau et al. 2013). As a consequence of weakened linkages between people and ecosystems, agrobiodiversity is being threatened and landscapes may become more vulnerable to crises and shocks (Brussaard et al. 2010). In this context, the quest now is how to balance trade-offs between resource use and conservation to design more resilient landscapes that guarantee the flow of ecosystem services to society with a minimum environmental impact (Bengtsson et al. 2003, Harvey et al. 2008, Melo et al. 2013). To support the planning of such landscapes, it is essential to understand how resilient agricultural systems and ecosystems are to different types and intensities of land use.

In the tropics, swidden cultivation, also called shifting cultivation, has transformed extensive landscapes into mosaics of cropping fields, agroforestry systems and secondary forests. The dynamics and sustainability of swidden cultivation is based on a balance between agriculture and forest recovery, representing an interesting system to evaluate management-environment interactions and to assess how such interactions can change under varying socio-economic conditions. Additionally, secondary forests play an essential role in these and other human-modified landscapes, as it also shelters high biodiversity levels and provides a range of goods to livelihoods (Lugo 2009).

The socio-ecological system studied in this thesis comprises the cassava-based swidden cultivation practiced by *caboclo* people in riverine Amazonia, Brazil. Swidden cultivation supports local livelihoods and supplies the staple food, cassava flour (*farinha* in Portuguese), of rural and urban populations in the Brazilian Amazon (Dias et al. 1998). In the last few decades, demographic and economic changes in riverine Amazonia (Parry et al. 2010a, Eloy et al. 2015) are changing the way these systems are managed (Emperaire and Eloy 2015), and encouraging agricultural intensification (Pereira and Lescure 1994). In swidden cultivation systems, agricultural intensification is the process of shortening the fallow period and increasing the frequency of swidden-fallow cycles in the same area. The aim of this thesis is to assess how agricultural intensification affects the resilience of swidden cultivation in the Brazilian Amazon. To achieve this objective I evaluate how landscapes and management practices are changing and how agricultural intensification affects swiddens productivity and secondary-forests recovery.

SWIDDEN CULTIVATION

Extensive areas of the tropics have been transformed by swidden agriculture into heterogeneous landscape mosaics of agricultural fields, successional forests, agroforestry systems and mature forests (Lawrence et al. 1998, Padoch 2010). Swidden agriculture, also known as swidden-fallow and shifting cultivation, is the main agricultural system supporting people's livelihoods in the Amazon (Padoch 2010). This system is based on the management of a diversity of crops, landraces, forest species and land covers, and is recognized as providing crop genetic diversity, biodiversity and knowledge conservation (Denevan and Padoch 1987, Padoch 2010). Swidden-fallow landscapes are essentially multifunctional, relying on the balance between cropping and fallow periods to provide nourishment and income to people (Denevan and Padoch 1987, Toledo and Salick 2006).

This system is traditionally managed by cutting and burning practices, with no use of external inputs, such as fertilizers or herbicides. Burning is an essential tool in low input systems, to make space for crops by clearing the field from laying logs and branches, and to provide short-term fertilization through the prompt release of nutrients from the forest biomass and the increase in soil pH promoted by the addition of ashes (Nye and Greenland 1960, Jordan et al. 1983). After ca. 2 years of cropping in the wet tropics, soil nutrients have either been uptaken by crops and weeds, leached down by the intensive rainfall, or been bound to the soil iron and clay particles (Nye and Greenland 1964, Jordan et al. 1983, Holscher et al. 1997). During this period weed infestation builds up increasing weeding labour demand (de Rouw 1995). At this point farmers usually decide to leave swiddens to fallow (Nye and Greenland 1964, Staver 1991, de Rouw 1995).

As soon as swiddens are harvested and abandoned for agriculture, secondary succession takes place through the vigorous regeneration of forest tree species combined with useful species remaining from the cropping period (Denevan and Padoch 1987, Uhl 1987). During the fallow period, secondary forests may continue to be managed for harvesting forest products such as timber, firewood, fruits, fibers and bush meat (Denevan and Padoch 1987, Dalle and de Blois 2006). Secondary forests are essential components of swidden-fallow systems, by fertilizing cropping fields (Nye and Greenland 1960, Johnson et al. 2001), suppressing weeds and pests (de Rouw 1995) and providing useful species and soil conservation (Denevan and Padoch 1987, Klemick 2011).

Fallow period can last for 10 years or more in traditional Amazonian systems (Nye and Greenland 1960, Coomes et al. 2000), but much variation is found among social, environmental and economic contexts (Silva-Forsberg and Fearnside 1997, Major et al. 2005) (Figure 1.1). Shorter fallow periods are practiced in richer soils, where regrowth is faster (Major et al. 2005), and under high population pressure (Metzger 2002, Schmook 2010, Coomes et al. 2011). The relation between the length of the fallow period and crop yields has motivated many studies, which found contrasting results (see Mertz 2002 for a review). Most of these studies did not account for the interaction between fallow regrowth and the number of times the field has been cut, burned and cultivated. The number of swidden-fallow cycles negatively affect the recovery rate of fallows (Gehring et al. 2005, Lawrence et al. 2010), and therefore may importantly affect the relation between fallow length and crop yield.

Agricultural intensification of swidden cultivation

Agricultural intensification is essentially a process of increasing input per unit of land per unit of time, and usually describes an increase in the efficiency per unit of product (Struik et al. 2014). As a concept, agricultural intensification has been applied in slightly different ways. It has been widely used as a synonym for a transition to modern agriculture by the use of chemical fertilizers, herbicides and mechanization, which usually results in higher yield per unit of land. Many studies use this definition when describing the intensification of swidden cultivation as the transition towards modern agriculture or permanent land uses (e.g., Schmidt-Vogt et al. 2009, van Vliet et al. 2012).

In the specific context of swidden cultivation, agricultural intensification has also been described as a process of increasing labour input, also known as input intensification (Boserup 1965). Agricultural (or input) intensification of swidden cultivation is characterized by an increase in the frequency of cropping cycles in the same field and consequently, the decrease in the length of the fallow period (see Erb et al. 2013). Accordingly, in this thesis I define agricultural intensification as the process of shortening the fallow period and increasing the frequency of swidden-fallow cycles in the same field (Figure 1.1), which is unrelated to the use of external inputs.

Swidden cultivation has been described as an extensive system that would only be intensified under high population pressure and land scarcity (Boserup 1965). In Asia, for example, the rapid increase in population sizes resulted in a wide collection of scientific research on the changes that swiddens were experiencing (see Mertz et al. 2009 for a review). Such studies showed that the drivers of intensification were not only related to population pressure but also to land tenure issues, market integration, labour availability and public policies (Padoch et al. 2007, Schmidt-Vogt et al. 2009). Consequences of intensification for swiddens included important changes in management practices that led to higher soil erosion, poor crop yield and lower availability of fallow products (Dalle and de Blois 2006, Ziegler et al. 2009, Erb et al. 2013).

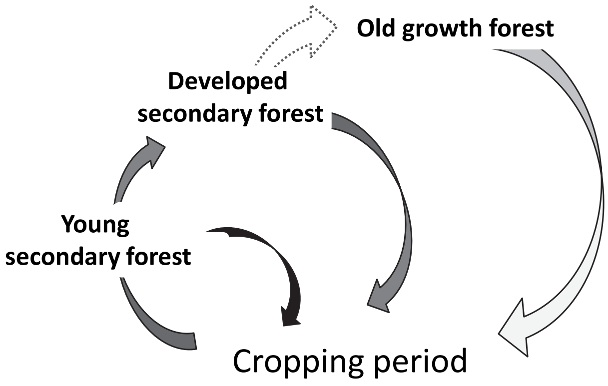

Figure 1.1. Shifting cultivation system showing the opening a field from old-growth forest (light grey arrow) and two types of fallow regime: a long fallow cycle (dark grey arrow) and a short fallow cycle (black arrow). In the Amazon, the length of the fallow period may vary from 5 years or less in intensified systems (black arrow) to more than 15 years in traditional systems. Eventually, secondary forests may be abandoned for agriculture and develop into old-growth forests (dashed arrow). In the Brazilian Amazon the cropping period lasts for one to two years and supports the production of bitter cassava.

In the Amazon, few studies have addressed agricultural intensification of swidden cultivation (Silva-Forsberg and Fearnside 1997, Coomes et al. 2000, Sirén 2007), maybe because intensification was not seen as an issue in a region where population densities are generally low. A recent synthesis has shown that transition in swidden cultivation in the Amazon follows different trends depending on the socio-economic context (van Vliet et al. 2013). At agricultural frontiers along roads, swiddens are being replaced for pastures and permanent agriculture, in response to drivers such as secure land tenure, access to market and population increase (van Vliet et al. 2013). On the other hand, in *caboclo* and indigenous communities, mainly located at riverine areas, swidden cultivation remains the main land-use system (van Vliet et al. 2013). Despite the persistence of swiddens in riverine Amazonia, the way such systems are being managed may be changing in response to recent socio and economic transformations.

Since the late 1970's, the distribution of riverine Amazonian populations is being reshaped by migration movements, the development of urban centres and changes in livelihood needs and aims (Parry et al. 2010a, Eloy 2015, Emperaire and Eloy 2015). People are concentrating on villages and are migrating from hinterlands towards the local urban centres in search for better access to education, health facilities, off-farm jobs and industrialized goods (Parry et al. 2010a). Alongside, the increase in urban population has raised the demand for agricultural products, such as the staple *farinha*. *Farinha* production relies on swidden cultivation practiced by smallholder farmers around cities and across riverine Amazonia (Dias et al. 1998). Market orientation and increased population density have driven traditional land-use systems towards agricultural intensification in other regions (Coomes et al. 2000, Sirén 2007) and may be affecting land use systems in riverine Amazonia as well.

SECONDARY FORESTS

Large extents of human transformed landscapes are covered by secondary forests. Secondary forests comprise the natural regeneration growing after an area has been abandoned for agriculture or cattle ranching. Estimations on the extent of secondary forests in the tropics are still missing, but in the Brazilian Amazon, where 18% of the original forest cover has been deforested (ca. 720,000 km^2), secondary forests were estimated to cover 150,000 km^2, comprising 21% of the deforested area until 2007 (Almeida et al. 2010, Embrapa and Inpe 2011). In the tropics, secondary forests regrow very fast (Letcher and Chazdon 2009), sequestering carbon at a rate up-to 20 times higher than old-growth forests (Pan et al. 2011, Bongers et al. 2015), and sheltering a high diversity of plants and animals (Chazdon et al. 2009), including many useful species for people (Toledo and Salick 2006). Nevertheless, the capacity of secondary forests to regrow and to provide such services depend on the land-use history of the sites (Chazdon 2003, Zarin et al. 2005, Lawrence et al. 2010). Therefore, understanding how resilient secondary forests are to different types and intensities of land use is key for elucidating the mechanisms underlying successional processes and for planning more sustainable landscapes.

Tropical forest succession

In the last decades, a great number of studies has contributed to reveal how the directional changes in tropical forest communities take place over time (Finegan 1996). Through time, there is a rapid increase in basal area, biomass, canopy height (van Breugel et al. 2006) and species diversity, and important changes in the taxonomic and functional composition of plant species (Chazdon et al. 2007, Lohbeck et al. 2012). Along the increasing complexity of the vegetation, the understory becomes more humid and darker (Lebrija-Trejos et al. 2011), with light availability greatly ruling species turnover (Denslow and Guzman 2000, Lohbeck et al. 2014). Despite these general patterns, common to tropical forests, the rates at which such changes take place and the set of species composing the plant community vary greatly among and within sites (Chazdon 2008). The sources of such variability remains to be determined, and has raised the interest in disentangling the relative importance of deterministic versus stochastic processes in ruling tropical secondary succession (Walker and Chapin 1987, Chazdon 2008, Norden et al. 2015). To move forward in this debate, it is necessary to gain knowledge on the sources of variation and on how different factors influence successional communities.

The fundamental sources of variation in successional communities are differential species availability and species performance (Pickett et al. 1987), both being influenced by an intricate set of factors. Species availability is dependent on the legacies left after disturbance, such as seed bank, sprouts and remnant trees (Uhl et al. 1981), and on dispersal limitation (Cubiña and Aide 2001). Both processes are defined by time since disturbance, land-use history (Uhl 1987, Mônaco et al. 2003), and landscape configuration (Holl et al. 2000, Cubiña and Aide 2001). Following species availability, succession will depend on species performance, which is defined by species life history strategies (Noble and Slatyer 1980), resources availability (Uhl 1987), and species interactions (van Breugel et al. 2011).

The relative importance of these factors in determining succession varies over time, along with vegetation-environment interactions (Walker and Chapin 1987, Lohbeck et al. 2014). Subsequently, it is hard to disentangle such effects through the widely used chronosequence approach (Walker et al. 2010b), upon which most of our knowledge on succession is based (Johnson and Miyanishi 2008). The chronosequence sampling design is based on the substitution of time for space, where stands with different ages since abandonment represent the changes in plant communities over time. An important assumption of this method is that initial conditions are similar, which not always could be assured, resulting in large deviations of chronosequence predictions from long-term measurements (Feldpausch et al., 2007; Johnson and Miyanishi, 2008; Walker et al., 2010b, Lebrija-Tejos et al. 2010). Therefore, to disentangle the effects of other important factors on plant communities, controlling for successional age would be helpful. In this sense, studying early stages of succession can greatly contribute to the overall understanding of how deterministic succession is. Early communities hold important information on further successional development, because they hold much of the species that will compose the community at later stages (Peña-Claros 2003). Moreover, the early species that form the canopy at the first ca. 20 years of succession (Finegan 1996), regulate environmental conditions in the understory (Kabakoff and Chazdon 1996, Lebrija-Trejos et al. 2011, Jakovac et al. 2014) and important biotic interactions (Walker et al. 2010a, Maggi et al. 2011) that will affect further species turnover. Another advantage of studying early stages is that the lower species diversity and high dominance by a few species makes the depiction of species – environment interactions more accessible. Therefore, different from most studies in secondary forests, in this thesis I did not use a chronosequence approach but I controlled for successional age, sampling same-aged secondary forest stands along gradients of land-use intensities, distances to the forest and soil conditions.

Land-use effects on secondary succession

Most secondary forests in the tropics are a result of human-driven transformations (Brown and Lugo 1990). Studies have shown that secondary succession can follow alternative pathways after different types and intensities of land use (Mesquita et al. 2001, Slocum 2001, Hooper et al. 2004). The relation between land use and forest succession is complex, though, because land-use effects are actually mediated by concomitant effects of management practices, landscape configuration, and site conditions, mainly related to modified soil properties. These three sets of factors have rarely been jointly assessed (but see Aragón and Morales, 2003; Lawrence, 2005b; Robiglio and Sinclair, 2011), and disentangling their role is essential to assess the mechanisms underlying land-use effects.

The main land-use types giving place to secondary forests in the tropics are pasturelands and shifting cultivation. On abandoned pasturelands, secondary forests emerge with reduced regrowth rate and species diversity, slow species turnover and different species composition (Mesquita et al. 2001, Peterson and Carson 2008, Williamson et al. 2014) when compared to shifting cultivation fields (Uhl et al. 1981, Holscher et al. 1997, Gehring et al. 2005, Vieira and Proctor 2007). Shifting cultivation has been considered as a low land-use intensity system, having been used as model to describe tropical forest succession (Uhl and Jordan 1984, Uhl 1987). Recent studies, however, have depicted important variations in recovery rate within shifting cultivation systems as a result of different intensities of use (Gehring et al. 2005, Lawrence et al. 2010). Therefore, not only land-use type but variations in the intensity of use within them must be assessed to understand land use effects.

In the wet tropics, where shifting cultivation and pasturelands are managed by slashing and burning practices, land-use effects on succession may be mediated by the selection for specific species traits like sprouting ability and fire-resistance (Hooper et al. 2004). It may also be mediated by modified soil properties, as recurrent fire can deplete nutrients and change soil physical properties (Palm et al. 1996, Lawrence et al. 2007, Runyan et al. 2012). Soil resources availability could affect species composition and species performance, as studies have shown that low fertility soils in general support lower biomass and growth rates (Uhl and Jordan 1984, Kanowski et al. 2003, Davidson et al. 2004, Lawrence 2005a). Additionally, in some situations, invasive species colonizing open sites can retard or even impede the successional process, through competition (Hooper et al. 2004, Schneider and Fernando 2010). At the landscape scale, land use changes may affect the amount and location of old-growth forests (Lawrence et al. 1998, Metzger 2002, van Breugel et al. 2013), strengthening species dispersal limitation and determining species availability (Butaye et al. 2001, Lawrence 2004, Robiglio and Sinclair 2011). These land-use underlying factors could act as ecological filters, selecting for specific species traits and restricting the range of successful species able to establish at new open sites (Lortie et al. 2004). Processes of ecological filtering, such as dispersal limitation and disturbance, have been shown to interact with the regional species pool to determine the species present in plant communities (Myers and Harms 2009). Consequently, in human-modified landscapes, underlying land-use factors may also act as filters to structure successional communities.

To assess how land-use affects succession it is essential to disentangle the individual and interacting roles of underlying land-use factors in structuring plant communities. Elucidating how land-use affects the resilience of secondary forests will contribute to advance the knowledge on forest succession (Peterson and Carson 2008), to improve management practices and to support land use planning in human-transformed landscapes.

RESILIENCE OF SOCIO-ECOLOGICAL SYSTEMS

Resilience theory offers a framework for understanding the response of dynamic and complex systems to disturbance. Ecological resilience is the capacity of ecosystems to absorb disturbances without changing its fundamental nature (Holling 1973, Walker et al. 2004). Resilience can be measured as the magnitude of disturbance that can be experienced before the system moves into a different state or condition (Holling 1973), i.e. it is the force required to push the system over the threshold that define alternative states. In theory, such thresholds are identified by abrupt changes in the characteristics of the system, but in practice abrupt changes have been rarely detected in open systems such as forests (maybe due to restricted spatial and temporal scales; but see Hirota, 2011), with gradual changes been more commonly found (Reyer et al. 2015). In forest ecology, resilience has been frequently operationalized as the recovery capacity, or the speed of recovery after disturbance (Van Nes and Scheffer 2007, Lawrence et al. 2010), and that is how the resilience of secondary forests is assessed in this thesis.

Another important aspect to understand the resilience of systems are feedback loops that can help or prevent the reorganization of the system or that trigger shifts in systems conditions (Folke et al. 2004). For example, in degraded areas in Hawaii, invasive grasses promote fire occurrence further favouring invasive species over native ones, maintaining the system in a degraded state (Mack and D'Antonio 1998). Whether the degraded state can be characterized as an alternative state is debatable (Suding et al. 2004), as delineating the boundaries of alternative states may be difficult in ecosystems with high diversity of species and interactions such as tropical forests (Reyer et al. 2015). Therefore, identifying feedbacks may be of great help in detecting important changes in system dynamics and species interactions that characterize a different condition (Folke et al. 2009).

The resilience approach is also being applied to understand the behavior of social systems in the face of shocks and crises (Berkes et al. 2002). In systems shaped by the interaction between people and nature, named socio-ecological systems, factors acting in different spheres such as management practices, cultural values and policy decisions play a role in the functioning of the system and in its capacity to reorganize after perturbations (Folke et al. 2009). In such systems, the definition of resilience is expanded to embrace the capacity of people to adapt to changing conditions and move forward (Berkes et al. 2002). Although adaptability is a human characteristic, it also depends on the environmental context, as some ecosystems may be more restrictive and allow less options for adaptation than others. Resilient socio-ecological systems are therefore those able to recover after disturbance/crises and to adapt, maintaining the functioning of the system (Berkes et al. 2002). Identifying thresholds and feedbacks can help understanding the resilience of socio-ecological systems and to operationally evaluate management requirements (Suding et al. 2004, Walker et al. 2004). Therefore, in a changing world, the concept of resilience offers an interesting approach for understanding how socio-ecological systems deal with changes and for planning more sustainable land-use systems.

The cassava-based swidden cultivation system

The socio-ecological system under study in this thesis is the cassava-based swidden cultivation practiced by *caboclo* people in the Brazilian Amazon (Figure 1.2). *Caboclos* are descendants of native Amerindian and Portuguese colonizers, who later mixed with north-eastern Brazilians who migrated to the Amazon during the rubber booms (1879-1912 and 1942-1945). *Caboclos* are the majority of river-dwelling

Amazonian population, whose livelihoods can be broadly distinguished between two main ecosystems: dwellers at white-water rivers, with access to large amounts of fish and to periodically enriched flooded areas (called *várzea*) for cultivation; and those at black-water rivers, where cultivation systems are exclusively located in non-flooded areas (*terra firme*), and fish resources are less abundant (Adams et al. 2009). This thesis focuses on *terra firme* communities, where livelihoods are mainly supported by resources provided by forests, agroforestry systems and swidden cultivation. Swidden cultivation supports several crops, such as corn, yam, pineapple and bananas, but predominantly the staple, bitter cassava (also called manioc, *Manihot esculenta* Crantz). Cultivation is based on manual and collective labour, with no use of external inputs such as fertilizers or herbicides, and takes place on swiddens of 0.5 to 3 ha (Figure 1.3).

Cassava cultivation is a cultural element of *caboclos* livelihoods, as it relates to people's knowledge of the ecosystem, the agrobiodiversity and diversification of landraces, with complex exchange networks as well as with the process of detoxifying bitter cassava (Emperaire and de Oliveira 2008). Exchange of cassava stalks among farmers, usually during collective work (Kawa et al. 2013), and the cultivation of different landraces within a field (from 7 up to 40 landraces, Emperaire and Peroni 2007), allow continuous cross-breeding and the creation of seedlings with new characteristics. These new landraces are then experimented and selected by farmers (Emperaire and Peroni 2007). The resulting collection of landraces embraces variations in maturation period (from 6 months to 2 years) and in performance under different conditions of weed pressure and soil fertility (Fraser 2010), for example. These characteristics allow for great flexibility on cultivation conditions and on harvesting season (Emperaire and Peroni 2007). Characteristics related to the food resource, such as the amount of starch and colour, are also considered during selection (Lima et al. 2012).

Bitter cassava is distinguished from sweet cassava by high concentrations of cyanogenic acid, higher yields in poor and acid soils and greater resistance to pest and pathogens (Wilson and Dufour 2002). To remove the cyanogenic acid, bitter cassava is processed into a toasted flour, named *farinha*, which is the staple carbohydrate that along with fish form the basis of the Amazonian diet. *Farinha* is produced for self-consumption and commercialization, the farmers being responsible for cultivating the cassava and processing it into *farinha* before selling (Figure 1.3). The main sources of income for the people in the study region are *farinha* and Brazil nut (*Bertholletia excelsa* Bonpl.), which are complemented by local trading of fish, hunt meat, fruits and timber (Pereira and Lescure 1994, Paiva et al. 2011, Lima et al. 2012). The market demand for *farinha* has increased in the last decades, promoting higher integration of swidden cultivators to the market (Pereira and Lescure 1994). In the region of the middle-Amazonas River, such integration is being more pronounced because it is one of the largest supplier of *farinha* to the capital, Manaus. Moreover, the *farinha* produced in this region is of a special type, called "*farinha do Uarini*" or "*farinha ova*", highly appreciated by the Amazonian people, and therefore, with a constant demand. This is the context of the socio-ecological system studied in this thesis (Figure 1.2).

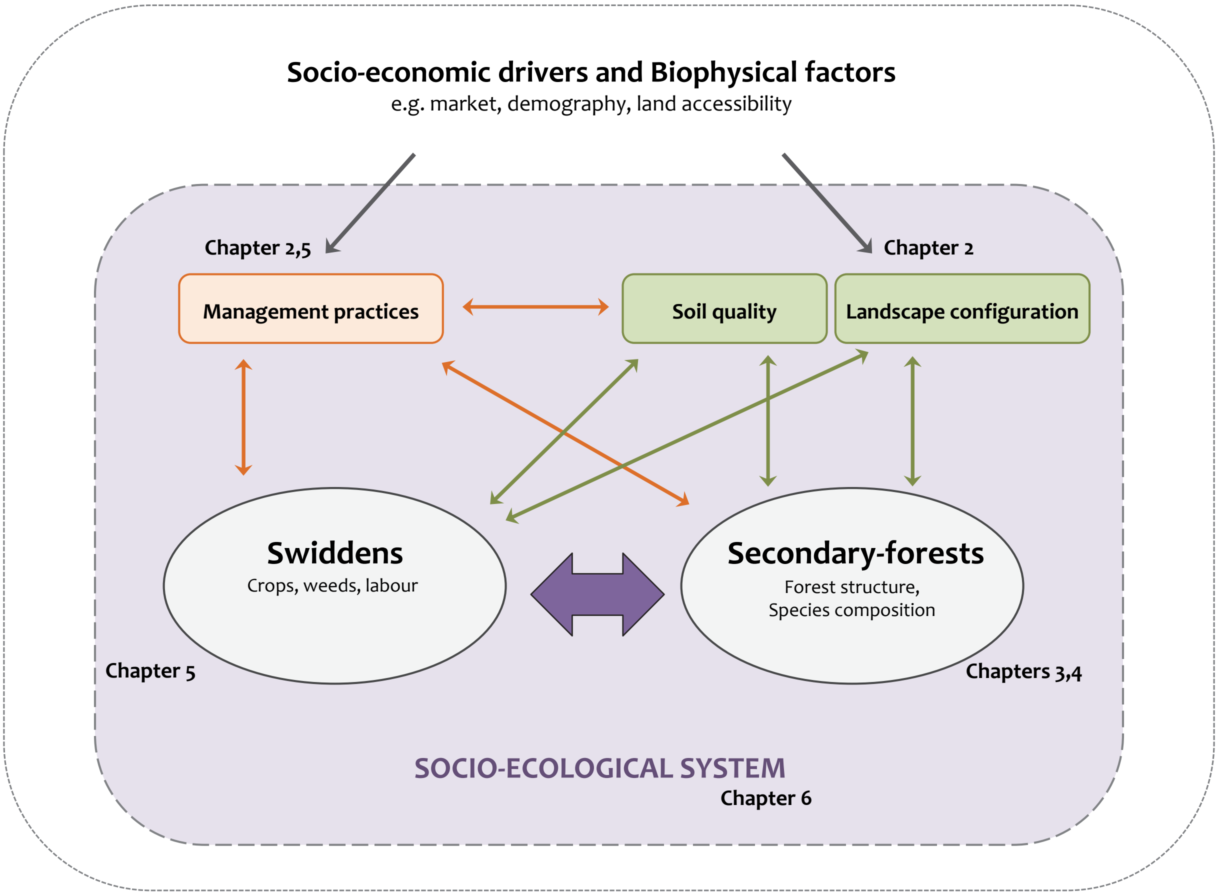

Figure 1.2. Conceptual framework used in this thesis representing the relationships among external drivers (external white box), human actions (orange box) and environmental conditions (green boxes) and their effects (solid arrows) on the swidden cultivation system (grey circles), which altogether compose the socio-ecological system studied in this thesis (dashed purple box). The system of interest is influenced by external forces, such as socio economic drivers and biophysical conditions, which consequences (black arrows) for management practices and landscape configuration were investigated in chapters 2 and 5. Management practices, soil conditions and landscape configuration affect the productivity of swiddens (Chapter 5), and the recovery of secondary-forest fallows (Chapters 3 and 4). The interaction among these elements, such as the interplay between swiddens and secondary forests (thick purple arrow) and their possible feedbacks on management practices, soil quality and landscape configuration are discussed in chapter 6.

Figure 1.3. Cassava cultivation and cassava flour (*farinha*) production in the region of the middle-Amazonas river, Tefé, Brazil. (a) Overview of the swidden cultivation landscape, showing the mosaic of agricultural fields and secondary forests; During the processing of cassava into *farinha*, cassava is soaked for two days (b). Next, cassava is pressed, grained and screened and then finally toasted in wood fired stoves in the casa de farinha (c); (d) cassava field adjacent to secondary forests dominated by the pioneer species *Cecropia concolor* and *Jacaranda copaia* at the back.

OBJECTIVES

The aim of this study is to evaluate the consequences of agricultural intensification for swidden cultivation systems in the Amazon. I evaluate how intensification-driven changes in landscape dynamics, recovery capacity, productivity and management practices can affect the resilience of the system. The specific objectives are:

(i) to assess if the dynamics of swidden cultivation landscapes have changed over time;

(ii) to reveal how agricultural intensification affects the resilience of secondary forests and the productivity of swiddens;

(iii) to evaluate what is the relative role of management practices, soil properties and landscape configuration in mediating land-use effects on secondary succession; and

(iv) to assess how management practices of swidden cultivation are changing with agricultural intensification.

To achieve these objectives I made use of ethnographic and bio-physical assessments and remote sensing methods. I used semi-structured interviews, participant observation and walking transects methodologies to assess current management practices and land-use history. To assess how agricultural intensification affects the recovery of secondary forests and the productivity of swiddens, I carried out field surveys along gradients of land-use intensity, represented by different number of swidden-fallow cycles.

STUDY AREA

This study was carried out in the municipalities of Tefé and Alvarães located in the region of the middle-Amazon River, in the Amazonas State, Brazil (Figure 1.4). Local and regional transportation is mainly done through the rivers network, with no roads connecting cities. Field surveys were conducted during the years of 2011, 2012 and 2013, in eight communities located within 70 km from the urban centers, along the Tefé river (Agrovila, Nogueira and São Sebastião) and the Bauana river (Vila Sião, São Francisco, Jauarituba and Monte Carmelo). The communities of Agrovila and Nogueira are the only ones connected by land to the urban centers, Tefé and Alvarães respectively. Tefé is the most important municipality in the region, with a population size of 62,662 inhabitants and density of 2.6 inhabitants per km^2 (IBGE 2013). Tefé is the second *farinha* producer in the Amazonas State, with ca. 96,000 ton of *farinha* produced per year (IBGE 2013).

The region is located at 100 m above sea level, with a mean annual temperature of 26^{0}C, total annual rainfall is between 2,500 and 2,800 mm. Climate is classified as tropical without a dry season (Af, Köppen classification), as rainfall in the driest month is $\geq$ 60 mm (Alvares et al. 2013). Vegetation in the non-flooded *terra firme* is classified as closed broadleaved ombrophilus dense forests (FAO-UN 1981). Soils are classified as oxisols and ultisols by USDA soil classification and as Acrisol by the World Soils reference database (WRB 2014). These soils are generally poor and acid, with low nutrient availability and high concentration of aluminum and iron (WRB 2014). Anthropogenic soils called Amazon dark earths are also found in this region but were not included in this study.

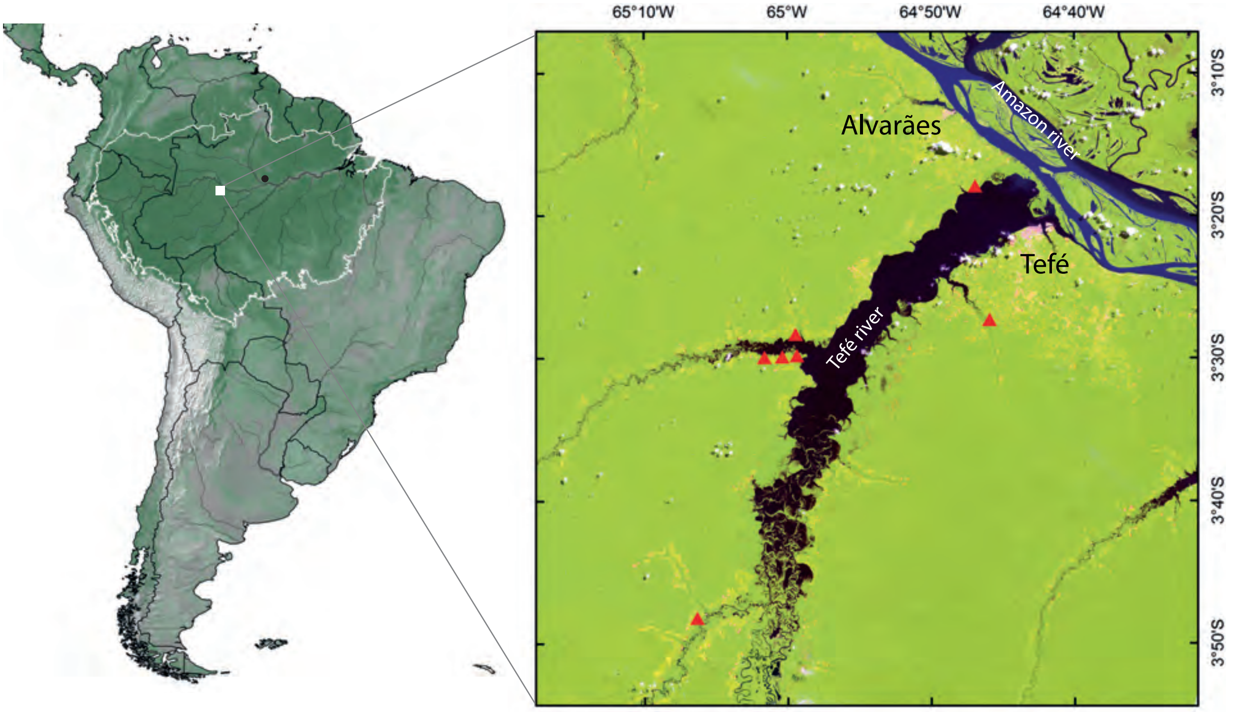

Figure 1.4. Map of South America indicating the Amazon basin (white line), the study area (black square) and the largest city, Manaus (white star), and a detail of the study area (Landsat image to the right). In the Landsat image, bare soil and urban areas are shown in pink colour, old-growth forest in dark green and secondary forest and agricultural fields in light green. The urban centres of Alvarães and Tefé are indicated, as well as the seven villages where the field work of this study took place (red triangles).

THESIS OUTLINE

This thesis is composed of six chapters: the introduction (Chapter 1), four research chapters (Chapters 2 to 5) and the general discussion (Chapter 6). In the four research chapters I evaluate the consequences of agricultural intensification for different components of the swidden-fallow system at the landscape (Chapter 2) and at the field level (Chapters 3, 4 and 5) (Figure 1.2). For that, I sampled fields along gradients of land-use intensity, defined by the number of past swidden-fallow cycles and the length of the previous fallow period.

In chapter 2, I evaluate if swidden cultivation systems are undergoing agricultural intensification, through the shortening of the fallow period and the increase in the number of swidden-fallow cycles. Through the collaboration with remote sensing researchers, I assess the temporal and spatial dynamics of swidden cultivation in the last three decades, in riverine landscapes of the middle-Amazonas river. Additionally, I test the hypothesis that intensification is associated with land accessibility, distance to villages and village size (Figure 1.2).

In chapter 3, I evaluate how agricultural intensification of swidden cultivation affects the resilience of secondary forests (Figure 1.2). In this chapter I define resilience as the recovery capacity of secondary forests, using as a reference the recovery level achieved by secondary forests subjected to the lowest intensity of use. Based on vegetation structure inventories, I evaluate the relative role of management intensity, soil properties and landscape configuration in determining the recovery of the structure of early-secondary forests. I test the hypothesis that the resilience of secondary forests decreases with land-use intensity.

In Chapter 4, I evaluate how land-use shapes species composition of secondary forests by investigating whether land use acts as a filter for species composition. I test the hypotheses that there are specific species assemblages associated with different land-use intensities and that increasing land-use intensity leads to a decrease in alpha and beta-diversity of the plant communities. Additionally, I assess how a specific trait, sprouting ability, of the species helps explaining species-environment relations.

In Chapter 5, I analyze how cassava yield, weed infestation, weed composition and weeding labour-demand (related to the type of weed and its rooting characteristics) change along gradients of land-use intensity. Additionally, I evaluate how swidden cultivation practices are changing, based on farmers interviews and available literature, and how agricultural intensification affects the productivity of swiddens. I test the hypothesis that agricultural intensification are leading to changes in management practices, to an increase in weed cover and weeding labour demand, and to a reduction in cassava yield. Finally, I discuss how changes in management practices may be related to market integration (Figure 1.2).

In Chapter 6, I integrate the findings of the research chapters with the societal context of the study area to evaluate how agricultural intensification is affecting the resilience of the cassava-based swidden cultivation system. I present a conceptual framework based on ecological filtering theory to describe how land use structures successional communities in human modified landscapes. I discuss how environment-management interactions can act as feedbacks that enhance the negative effects of agricultural intensification on the swidden cultivation system. Finally, I reflect on the challenges and opportunities of the *farinha* market and provide recommendations to maintain and enhance the systems' resilience, considering the social and ecological context of riverine Amazonia (Figure 1.2).

Chapter 2

Spatial and temporal dynamics of swidden cultivation in the middle-Amazonas river: expansion and intensification

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Submitted for publication

ABSTRACT

Swidden cultivation is the traditional agricultural system in the Amazon. In the last four decades riverine Amazon have undergone important socio-economic transformations that may have resulted in land use and land cover changes. We investigated the temporal and spatial dynamics of swidden cultivation in riverine landscapes during the last 30 years to identify changes in the rates of agricultural expansion and intensification during this time period. Additionally, we evaluated how land accessibility determines land use and land cover at present landscapes. We applied a novel remote sensing technique to retrieve the temporal dynamics of swidden-fallow fields. By applying the breakpoint-detection algorithm to Landsat time-series over three decades (from 1984 to 2013), we identified slash-and-burn events of fallows or old-growth forests and estimated the time interval between two of these events. Our results show that swidden cultivation in riverine communities of the middle-Amazonas river has gone through a process of agricultural intensification in the last 30 years. Through time, swiddens expansion over forest has slowed down and fallow period length has decreased on average from 9 to 5 years. Expansion and intensification were associated with land accessibility, with fields being mostly located within 2 km around settlements, and with shorter fallow periods and higher frequency of cycles been practiced closer to the settlements housing area. These findings show that along with recent socio-economic transformations in riverine livelihoods, the dynamics of swidden cultivation is also changing. Understanding land use dynamics can support land-use planning policies and improve estimations of the potential of these landscapes to provide ecosystem services.

KEY WORDS: Brazil, breakpoint detection, cassava, fallow, land cover, land use, remote sensing, time-series

INTRODUCTION

Tropical landscapes have been largely transformed by human land use. Swidden cultivation plays a central role in land cover transformation given its widespread occurrence in the tropics (van Vliet et al. 2012). Through time and space, swidden cultivation systems have undergone expansion and intensification phases following public policies and socio-economic changes in the tropics. From the 1960s to the 1980s, swidden cultivation systems were expanding over forest following government policies that stimulated the colonization of agricultural frontiers in Asia and Latin America (Rudel et al. 2009). Subsequent public policies discouraged swidden cultivation practices and triggered, together with population increase and other socio-economic drivers, agricultural intensification and the replacement of swiddens for permanent land uses (Padoch et al. 2007, Fox et al. 2009).

Processes of expansion and intensification in swidden agriculture have been widely reported for Asia (for a review see Mertz et al. 2009), but less so for the Amazon (Vosti et al. 2002, Brondizio 2009, van Vliet et al. 2013). The overall low population densities in the Amazon have raised little concern and scientific attention to land use and land cover changes related to swidden cultivation, which remains the main agricultural system in riverine areas (van Vliet et al. 2013). Despite the apparent large availability of land in riverine Amazon, access restrictions may play an important role in ruling actual land availability and resource use in these areas where land is accessed by walking and through permanent and intermittent rivers (Coomes et al. 2000, Castella et al. 2005, Salonen et al. 2012). Additionally, in the last four decades riverine Amazon is experiencing important changes in its socio-economy and demography (Brondizio 2009), with rapid urbanization and increased demographic concentration around villages and around the local urban centres (Padoch et al. 2008, Parry et al. 2010a). Coupled to the urbanization process, market demand for cassava flour (*farinha*, in Portuguese), the staple food in the Brazilian Amazon, is increasing and is leading to changes in traditional agricultural practices (Emperaire and Eloy 2015, Jakovac et al. *submitted*). Since migratory movements, market demand and price changes have been historically important determinants of social changes with strong implications for land-use in the Amazon (Brondizio 2009, Vogt et al. 2015), it is expected that these forces are also affecting land use patterns and encouraging agricultural intensification in riverine Amazon.

In this study, we investigate the temporal and spatial dynamics of swidden cultivation in the region of the middle-Amazonas river to evaluate how swidden agriculture has expanded and/or got intensified in the last three decades. The middle-Amazonas river is one of the largest cassava flour producing region in the

Brazilian Amazon, and is experiencing strong market orientation following the increasing market demand for *farinha* (Pereira and Lescure 1994, Jakovac et al. *submitted*). We hypothesized that swidden agriculture in the middle-Amazonas river has become more intensified in the last three decades and that land accessibility plays an important role in determining expansion and intensification patterns.

To detect land cover dynamics, most methods rely on land cover classification and bi-temporal changes, i.e. compare the land cover in two moments in time (e.g. Coppin et al. 2004). While these methods are useful to detect major changes in deforestation and the spatial distribution of agricultural fields, they are limited in recognizing changes in dynamic systems in the tropics. Rapid vegetation regrowth limits the ability of bi-temporal methods to distinguish cropping fields from secondary forests, for example, restricting its capacity to detect land use dynamics (Coppin et al. 2004). Such limitations represents a major constraint for detecting temporal dynamics of swidden-fallow cultivation in the tropics (Li et al. 2014). Therefore, aiming to detect temporal dynamics of the swidden cultivation system, we used a novel remote sensing method to retrieve the frequency of slash-and-burn events and the length of the fallow period. We applied an algorithm that detects breaks in remote sensing time-series (Bai and Perron 2003, Zeileis et al. 2003), allowing for the detection of small scale disturbance in the vegetation, such as clear-cut events (DeVries et al. 2015). Variations of this method have been recently applied to monitor disturbance in old-growth forests (DeVries et al. 2015, Dutrieux et al. 2015), and are considered promising to overcome the challenge of detecting land cover change in highly dynamic systems in the tropics (Asner 2001, Asner et al. 2004, Li et al. 2014).

From remote sensing time-series we retrieved and mapped the history of clear-cut events of swidden-fallow fields during the last three decades (1984 to 2013), to evaluate if fallow periods have changed through time and how this change relates to distance to settlements and settlements size. Additionally, we describe the current swidden-fallow fields of the study area, in terms of land-use intensity and age distribution of secondary forests in 2013. Understanding how swidden cultivation systems are being transformed in riverine Amazon is essential to support land-use planning policies and to improve estimations of the potential of these landscapes to provide ecosystem services.

METHODS

Study site

This study is focused on the municipalities of Alvarães and Tefé, located at the region of the the middle-Amazonas river. Tefé is the most important municipality in the region, with a population size of 62,662 inhabitants and density of 2.6 inhabitants per km^2 (IBGE 2013). Tefé is the second cassava-flour (*farinha*) producer in the Amazonas State, with ca. 96,000 ton of *farinha* produced per year (IBGE 2013). *Farinha* is the staple food in the Brazilian Amazon. It is produced from bitter-cassava cultivated on swidden cultivation systems by *caboclos*, which are mixed blood people (Adams et al. 2009). Swidden cultivation in the study area is supported by family labour, with no use of external inputs such as fertlizers and herbicides, and is meant for subsistence and commercialization (Jakovac et al. *submitted*).

This study is focused on riverine communities located within 50 km around the urban centre of Tefé. For retrieving land-use history, we delimited the study area as the area accessed by rivers and not connected by roads to the urban zones, covering 4 km from the large river margins (Tefé and Bauana rivers) and 3 km from small tributaries, covering an area of 55,120 ha of upland surface. We assured that this delimited area included all deforestation mapped by PRODES (INPE 2013). To characterize the study area, we used the land cover maps provided by the Brazil's monitoring program of deforestation in the Legal Amazon - PRODES (INPE 2013). From PRODES maps we extracted the area covered by forest and the accumulated deforestation until 2013, which represents the area under influence of land use. We assessed the location of settlements and the number of households during field expeditions in 2012 and 2013 (Jakovac et al. 2015) and complemented this information with secondary data (Parry et al. 2010a). The rivers network was sourced from Hydroshed (Lehner et al. 2008).

Mapping land-use history

To retrieve the land-use history of the swidden-fallow fields, we applied a method that detects breaks in remote sensing time-series (Dutrieux et al. *in review*). The method combines a break detection algorithm derived from the econometric literature (Bai and Perron 2003, Zeileis et al. 2003), with a multi-temporal spatial segmentation (Desclée et al. 2006), to provide information at the individual swidden-fallow fields scale. The main steps of the method consist in (i) assembling multiple layers of Normalized Difference Moisture Index (NDMI) derived from 30 m resolution Landsat data into time-series, (ii) segmenting the area by grouping neighbouring pixels having similar land use trajectories, (iii) detecting break points in the NDMI time-series for each segment independently and (iiii) classifying the detected breaks according to the change-process they represent. The detected breaks represent changes in land use regimes, such as clear-cuts (i.e. slash-and-burn event) or land abandonment/stabilisation (Appendix-Figure A2.1; e.g. DeVries et al. 2015). Once we know, for each field, the dates when the clear-cut breaks happened during the monitoring period, we can retrieve the number of times the field has been cultivated and the duration of the fallow period.

The method was validated against information from farmers interviews, and proved to predict the number of swidden-fallow cycles with an accuracy of 1.2 cycles (corresponding to a Normalized Root-Mean-Square Error (NRMSE) of 0.41) and the length of the fallow period with an accuracy of 1.3 years (NRMSE = 0.19) (Latifah 2015). We applied the method on a time-series of 324 Landsat images spanning the 1984-2013 period. Because a minimum number of observations is needed for a breakpoint to be detected across the time-series profiles, no clear-cut breaks could be detected before 1987 and after 2012. A complete description of the method can be found in Dutrieux et al. (*in prep.*). Additionally, to know the land cover at the start of the monitoring period, we classified a reference image of 1984 (Landsat image from August 9th, 1984) into six land cover classes: old-growth forest, agricultural field (including fallows and cropping fields), bare soil, cloud, shadow and water.

Sampling the swidden-fallow fields

To apply further statistical analyses, we sampled the area classified as deforested in PRODES land cover maps, by locating 4,488 random points and allowing a minimum distance of 70 m between points, to avoid sampling the same agricultural field twice. For each sampled point (referred as *sampled location* from now on) we extracted the information on the land-use history, and calculated the Euclidean distance to the centre of the nearest settlement housing-area (referred as *distance to settlement* from now on) using ArcGIS 10.1 (ESRI 2012).

Based on the land-use history retrieved for swidden-fallow fields, we extracted the following parameters: dates of clear-cut breaks and time interval between subsequent clear-cut breaks. Based on the dates of the clear-cut breaks we assessed (i) the date of the first clear-cut event detected, (ii) the length of the fallow period through time, which was calculated as the time interval between subsequent breaks subtracting two years that corresponds to the usual cropping period practiced in the study area (Jakovac et al. *submitted*), and (iii) the age of the secondary-forest fallow in 2013, calculated as the interval between 2013 and the date of the last clear-cut break detected, subtracting two years of cropping period. We also assessed the total number of swidden-fallow cycles at each sampled location by counting the clear-cut breaks detected from 1984 to 2013.

Data analyses

Characterizing the present swidden-fallow fields

We characterized the landscape of the study area into old-growth forest (including floodplain) and accumulated deforestation until 2013, based on PRODES land cover map (INPE 2013). Within the deforested area, we characterized the land-use history of the swidden-fallow fields, which was assessed through the remote sensing segmentation algorithm.

Based on the sampled locations, we described the current swidden cultivation fields according to the (i) percentage of sampled locations currently at the cropping phase, i.e. ≤ 2 years since the clear-cut break detected, (ii) the percentage of sampled locations at the fallow phase, i.e. > 2 years after the clear-cut event, (iii) the age of the secondary-forest fallows (calculated as the interval between 2013 and the last clear-cut event) and (iv) the total number of clear-cut events from 1987 until 2012. Then we evaluated the relation between land accessibility and age of secondary forests and the number of swidden-fallow cycles by fitting mixed effects models. We included as dependent variables the age of the current secondary forest and the number of swidden-fallow cycles. As fixed factors we included the distance to the nearest housing area (continuous variable) and the settlement size (categorical variable). Settlements were included as random factors. Settlements were classified according to the number of households: isolated households (1-3 houses), small village (4-10 households), medium size village (11-29 households), and large villages (> 30 households).

Characterizing swiddens expansion

To evaluate if the expansion of swidden cultivation over mature forest has changed through time, we calculated the number of first-clear-cut events identified at each year. To validate the changes in expansion rate over time, we calculated the yearly deforestation rate for the study area, based on PRODES land-cover maps, which provides cumulative deforestation up to 1997 and annual deforestation from 1998 onwards (INPE 2013).

Evaluating changes in fallow-period length over time

To evaluate if the length of the fallow periods have changed over time and how it is related to accessibility, we applied a survival analysis (Therneau and Grambsch 2000), which has been applied before for this purpose elsewhere (Coomes et al. 2000, Vance and Geoghegan 2002). This analysis estimates the survival probability of subjects that have been monitored through time and which could have experienced none, one or multiple events during the monitoring period. In this study, the probability of survival refers to the probability of a sampled location to continue as forest (old-growth or fallow), and the event of interest is the clear-cut break, which represents the end of the fallow and the start of the next cropping period. In this analysis, the time period between the last event and the end of the monitoring period (2013) is taken into account as "censored" data (Therneau and Grambsch 2000).

We first evaluated if fallow period has changed over time by testing the hazard rate proportionality, based on the Schoenfeld residuals of a Cox regression model (Therneau and Grambsch 2000). We fitted the Cox regression with multiple events per sampled location, and considering censored data to the right. Sampled locations were included as clusters, distance to settlement as an independent variable (continuous) and settlements size as a stratum. We then tested the hazard rate proportionality, i.e. if the probability of forests/fallows being cut changed over time. We fitted Cox model using the *coxph* function and tested hazard rate proportionality using the *cox.zph* function of the *survival* package for R (Core-Team 2013).

Given that hazard rate proportionality is an assumption of survival regression models, if hazard rate changes over time, a non-parametric test should be applied to compare the effect of groups on the probability of survival. Consequently, we fitted Kaplan-Meier survival curves, and applied log-rank tests, to evaluate if the probability of a fallow not being cut changes with distance to settlement and with settlement size. We categorized the distance to settlement into 4 classes: ≤1 km, 1 - 2 km, > 2 - 3 km and > 3 km. We fitted survival curves with the function *survfit* and tested log-rank differences with *survdiff* from the *survival* package for R (Core-Team 2013).

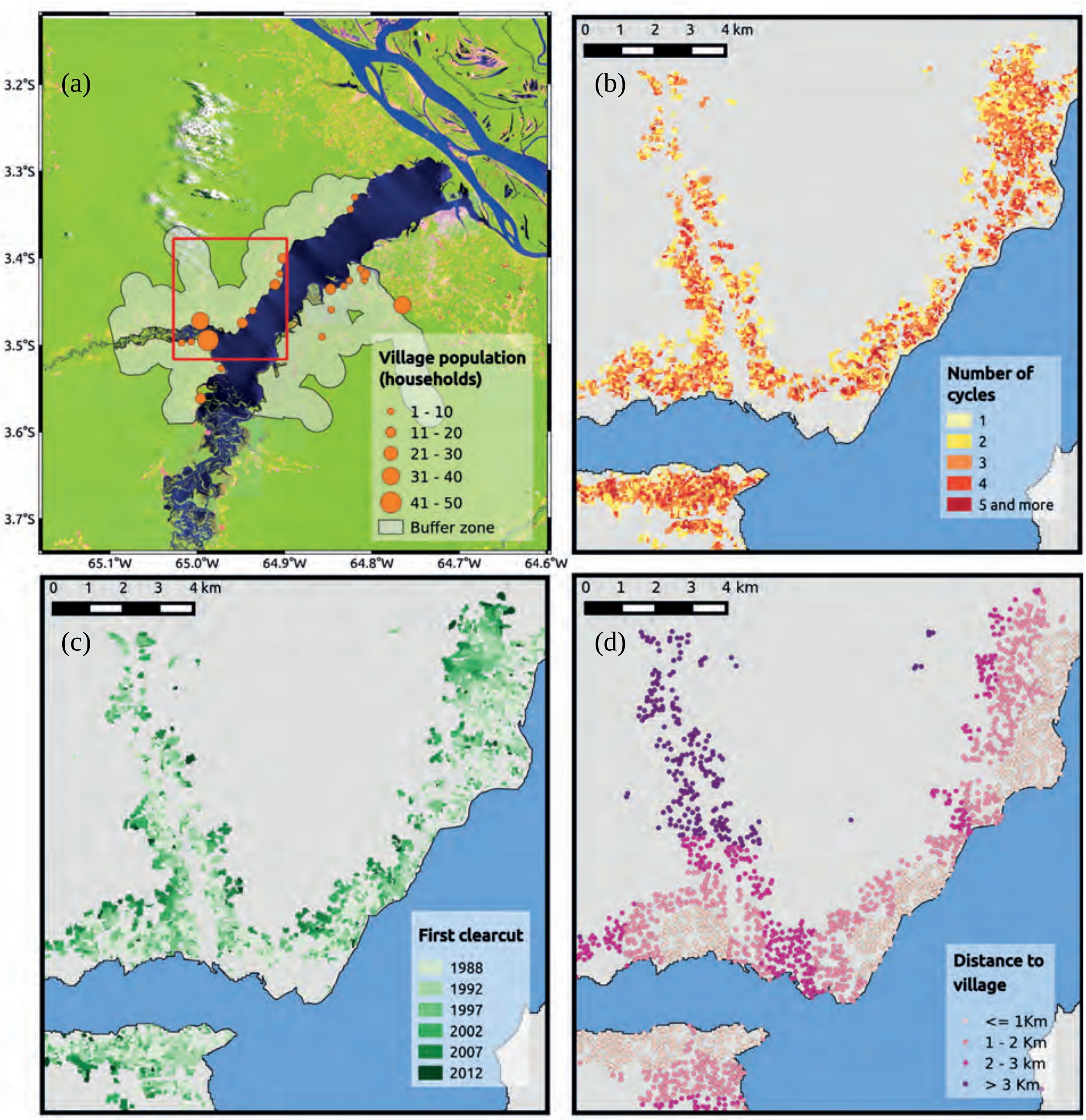

Figure 2.1. Map of the study area. (a) Landsat image of the study area (buffer zone) showing the location of riverine communities and respective number of households. The orange square indicates the zoomed area represented in maps b, c and d. Maps show the land-use history of agricultural fields during the time period of 1984 until 2013, retrieved through the breakpoint detection method. Segments represent pixels that have similar land-use history and therefore represent the agricultural fields; (b) Map of the number of clear-cut events (swidden-fallow cycles) detected during the whole monitoring period at each segment; (c) Map of the date when the first clear-cut event was detected at each segment; (d) Map of the random points located for sampling the agricultural fields. Colours indicate the four distance classes from settlements housing-area.

RESULTS

The study area covers 55,120 ha of upland area and comprises 22 settlements of different sizes, varying from a single household up to 50 households (Figure 2.1a). According to PRODES land cover maps, 78 % of the study area is covered by old-growth forest (42,838 ha) and 22% have been deforested until 2013 (12,280 ha), and comprise the area under influence of land use. From the 4,488 sampled locations within the area under influence of land use, 50% (2,266) had no clear-cut break detected during the monitoring period. According to the reference image, most of these locations (67%; 1,510 samples) were old-growth forest in 1984, and therefore may correspond to small remnant forest patches. A few of these samples with no clear-cut break detected, were already deforested in 1984, and are located around the settlements' housing area (18%; 417 samples). The remaining 15% (339 samples) could not be classified in the reference image due to cloud coverage, and may correspond to other land use types such as home gardens and agroforestry systems.

The additional 50% of the sampled locations had one or more clear-cut breaks detected during the 25 years monitored, and correspond to the swidden-fallow fields (2,222 samples) (Figure 2.1b). Most of these locations were classified as old-growth forest in the reference image of 1984 (75%; 1,663 samples), and therefore had their land-use history fully retrieved (i.e. since deforestation) by the remote sensing time-series. Only 20% of the samples (452 sampled locations), were already deforested in 1984 and therefore had experienced one or more clear-cut events before the monitoring period started. The remaining locations could not be classified in 1984 due to cloud coverage (5%; 107 samples).

Current swidden-fallow fields

The swidden-fallow fields are located along the large rivers and small tributaries (Figure 2.1a,b), with 80% of the fields comprised within 2 km from settlements (2.06 ± 1.65 km; Mean ± SD) (Figure A2.2). This 2 km distance is mostly accessed by foot, while areas further than 3 km from settlements are accessed through small river tributaries (Figure 2.1d). Currently, the fields are mainly covered by secondary-forest (84 %; 1,838 sampled locations), with only 16% of the sampled locations being at the cropping phase (359 samples). Most of the secondary-forest fallows (80%) were < 10 years old in 2013 (Figure 2.2a). Accounting for the number of past swidden-fallow cycles, 81% of the sampled locations (2,076) had experienced ≤ 3 clear-cut events within 25 years monitored (Figure 2.2b).

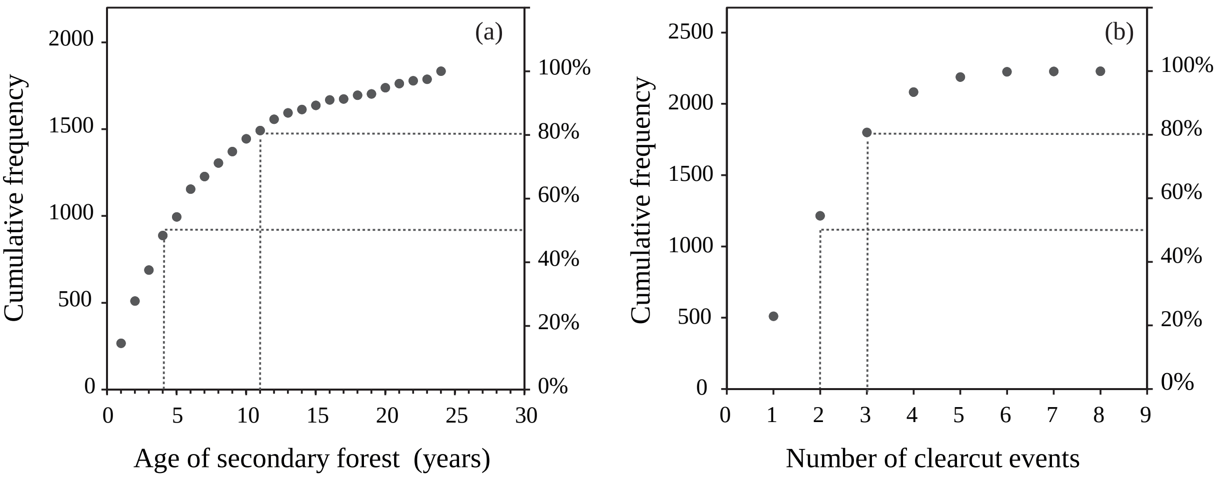

Figure 2.2. Secondary forest age and land-use intensity of the swidden-fallow landscape in 2013. A) Cumulative frequency of sampled locations on secondary-forest fallows with different ages in 2013. B) Cumulative frequency of sampled locations that experienced different number of clear-cut events (swidden-fallow cycles). Data based on 2,222 sampled locations that had at least one clear-cut event detected during the monitoring period.

The age of the fallow and the number of clear-cut events were significantly related to distance to settlements and settlement size (Table A2.1). The age of current secondary-forest fallows increased with distance to settlements (GLMM, Df= 2198, t-value= 2.75, p=0.005) and was higher around isolated households than around villages, regardless of their size (DF= 18, t-value=4.47, p=0.003; Table A2.1). Number of clear-cut events decreased with distance to settlements (GLMM, Df= 2198, t=-5.88 , p<0.001), and was not affected by settlement size, being only marginally lower around isolated households (GLMM, Df= 18, t= -1.79, p=0.08; Table A2.1).

Expansion of swidden-fallow fields

The expansion of swiddens over old-growth forest was higher between 1988 and 1991 and then slowly decreased over time, shown by a decrease in the frequency of first-clear-cut events (Figure 2.3). The decrease in the frequency of 1^{st} clear-cut events along with an increase in total number of clear-cut events, indicates that more fields are being opened each year, but mostly on fallows and less on old-growth forests (Figure 2.3). Recent expansion of swiddens occurred sparsely, mainly in the borders of the agricultural areas around settlements and upriver along small river tributaries (Figure 2.1c). Similarly, deforestation estimations retrieved from PRODES land-cover maps indicated that 83 % of the total deforestation detected in the study area occurred before 1997 (10,070 ha) and only 17% occurred between 1997 and 2012 (2,210 ha).

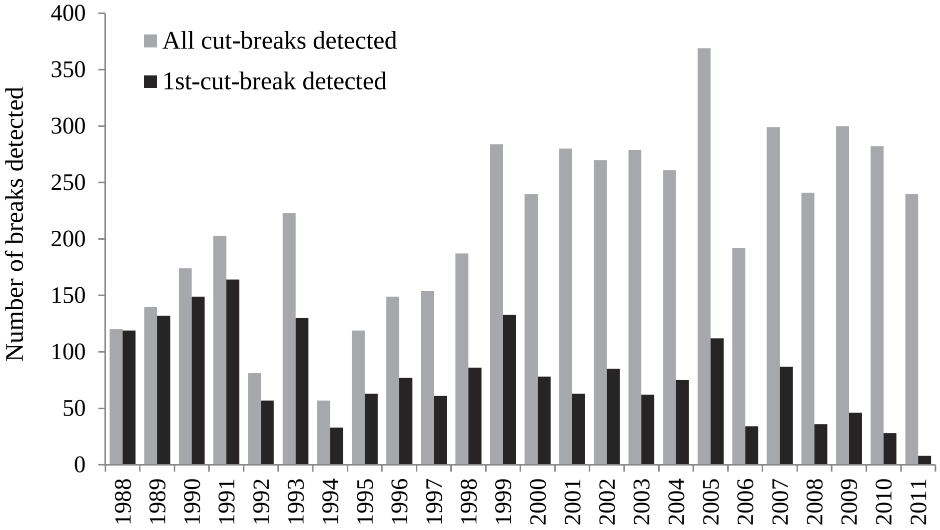

Figure 2.3. Frequency of clear-cut events and first clear-cut event detected each year, over time. Frequency based on 2,222 sampled locations that had at least one clear-cut event detected within the 30 years monitoring period.

Changes in fallow-period length

The hazard proportionality test indicated that the probability of fallows been cut (the hazard rate) increased over time (rho= 0.067, Chi^2= 49.3, p<0.001; Figure A2.2), which can also be detected by the crossing of survival rate curves (Figure 2.4). The fitted survival curves showed that the probability of a fallow been cut significantly decreases with distance to settlements (Chi^2=159, p<0.001, df=3), being lower at < 1 km, intermediate at 1-2 km and 2-3 km, and higher at ≥ 3 km (Figure 2.4a). The probability of a fallow not been cut was also different among settlement sizes (Chi^2=259, p<0.001, df=3), being higher around isolated households than around villages regardless of their size (Figure 2.4b).

Through time, the difference in the survival probability among distance classes from settlements decreased due to an overall reduction in fallow period in the last decade (Figure 2.5). The percentage of sampled locations followed up by short fallow cycles (< 5 years) increased through time in all distance classes (Figure 2.5). Within 1 km from settlements, fallow period decreased from on average 9 years before the 1990's to 5 years after 2000, while at distances longer than 3 km, fallow period decreased from 12 years to 5 years in the same time period.

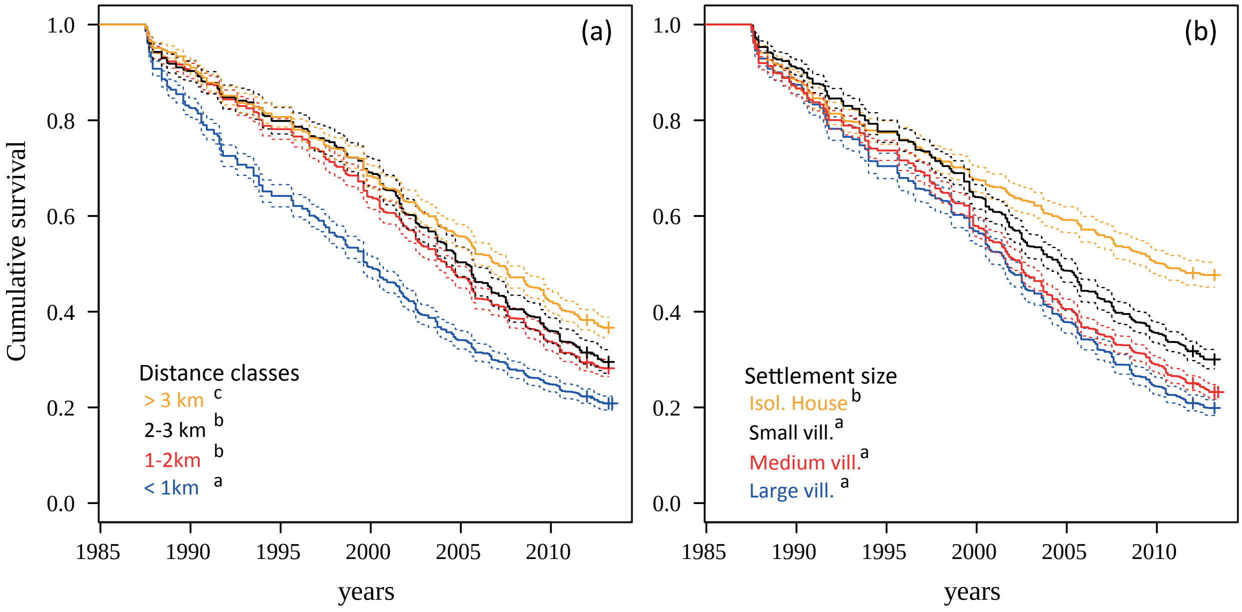

Figure 2.4. Kaplan-Meier survival curves for sampled locations at different distances from settlements (A) and at settlements of different sizes (B). Cumulative survival probability of fallows refers to the probability of fallows not been cut. Monitoring period spans from 1984 to 2013. Distance to settlements was classified as < 1 km, 1- 2 km, > 2- 3 km and > 3 km from the nearest settlement. Settlement size was categorized by the number of households: isolated households (1-3 houses), small village (5-10 households), medium size village (11-29 households), and large villages (>30 households). Results of log-rank pairwise comparisons between groups are presented by superscript letters next to the legend, considering Bonferroni-corrected alpha = 0.008.

Figure 2.5. Percentage of short and long fallow periods over time and across distance classes from the housing area. Bars represent the proportion of fields that were followed up by short (< 5 years) and long (> 5 years) fallow periods over the years of 1988 until 2006, at each distance class to the settlement housing area. Information after 2006 was not included to avoid bias due to the ending of the monitoring period in 2013.

DISCUSSION

By using a novel remote sensing technique we could assess the dynamics of swidden cultivation fields through time with high temporal and spatial scales. Our data show that in the last 30 years, the expansion of swiddens over old-growth forest has slowed down through time, while swidden cultivation has been intensified, through the shortening of the fallow period. Our data support that fallow period length is associated with access and suggest that constraints of land accessibility are encouraging agricultural intensification. These findings reveal that the dynamics of swidden cultivation is changing in the Amazon, possibly following recent socio-economic transformations in riverine livelihood related to the cassava market and migration movements (Parry et al. 2010a, Emperaire and Eloy 2015).

The results show that the highest expansion rate of swiddens over old-growth forest occurred in the late 80's and early 90's (Figure 2.1c, Figure 2.3), which coincides with the increase in human population in the studied municipalities: 1.2 times increase between 1980 and 1991 vs 0.2 times between 1991 and 2010 (Figure A2.4; IBGE 2013). After this period, the expansion of swiddens has slowed down (Figure 2.3), coinciding with an overall decrease in the fallow period length (Figure 2.4, Figure 2.5), from ca. 9 to 5 years on average during the study period. Interestingly, such agricultural intensification is occurring mainly around villages, with isolated households showing an opposite trend (Figure 2.4b). The increase in the length of fallow period around isolated households through time is possibly a result of out-migration and the abandonment of fallows upriver. These results agree with demographic changes reported for this and other riverine areas that have experienced depopulation in the hinterlands and increased population concentration around villages, mainly villages close to the urban centres (Parry et al. 2010b).

Our results show that agricultural intensification is associated with land accessibility. On one hand, easily accessible areas are more intensively used, so that throughout the last 30 years, the fallow period has been shorter closer to the housing area (< 1 km) than farther away (Figure 2.5). This finding agrees with other studies showing a gradient of land use types and intensities with distance to the housing area (Lawrence et al. 1998, Sirén 2007, Dalle et al. 2011). At the same time, access limitation encourages shorter fallow periods because the transport of harvested cassava to the processing place (*casa de farinha*), and of *farinha* to the houses, is done manually. Even when swiddens are reached through small river tributaries, the effort to carry the produce is high as most tributaries are not navigable during the dry season (Salonen et al. 2012). As the location of swiddens is constrained by accessibility, farmers might decide for shortening the fallow period over carrying the produce longer distances (also shown elsewhere by Dalle et al. 2011). Inhabitants of the study area acknowledged that fallow period has been recently shortened because "forest is too far" to open new fields (also reported for other areas by Siren 2007, Parry et al. 2010a). But how far is too far? We found that most of the swidden-fallow fields (80%) are accessed by land within 2 km from the housing area (Figure A2.3), and that most of the new fields are being opened upriver along small tributaries (Figure 2.1c). These patterns indicate that 2 km from the housing area may correspond to a walking distance threshold that encourages intensification. These findings confirm the association between accessibility and land cover change and land-use patterns (Castella et al. 2005, Soler et al. 2009, Dalle et al. 2011, Barber et al. 2014).

Along with land accessibility, other factors related to socio-economic changes, policies, regulations and land tenure may also play a role (Boserup 1965, Coomes et al. 2000, Sirén 2007, Lambin and Meyfroidt 2011). According to other studies, major changes in the socio-economy of riverine areas have been related to the resettlement of rural population around villages and increased market integration (Parry et al. 2010a, Kawa et al. 2013, Emperaire and Eloy 2015). Moreover, market demand for *farinha* has been sharply increasing along with its price over the last decade, with a price increase of 398 %, against an accumulated inflation of 72.3 %, for the same period (Triami BV, 2015). Increasing market demand and prices might stimulate cassava cultivation, both for commercialization and subsistence, as living costs increases along with staple food prices (Kawa et al. 2013). Market effects along with increased population concentration and land accessibility constraints are probably associated with the process of agricultural intensification in the middle-Amazonas river.

As a result of agricultural intensification, the landscape is becoming simplified and with the predominance of young secondary forests (80% is less than 10 years old; Figure 2.2c), indicating a trend of developed secondary forests to disappear from the landscape (Metzger 2002). Repeated cycles within a short fallow period regime results in important decreases in secondary forest regrowth rate and in swiddens productivity, which all together jeopardizes the sustainability of swidden landscapes (Jakovac et al. *submitted*). Moreover, ephemeral secondary forests play a restricted role in the conservation of tree species (van Breugel et al. 2013), carbon sequestration (Johnson et al. 2001, Kauffman et al. 2009) and the provision of forest products (Dalle and de Blois 2006). Given that swiddens are responsible for the formation of most secondary forests in riverine Amazon (Almeida et al. 2010), intensification may undermine the potential contribution of these landscapes to the provision of ecosystem services.

The use of breakpoint detection over Landsat time-series allowed us to detect changes in land use dynamics of agricultural fields with a high temporal and spatial resolution over a long time period. Our results show that intensification and expansion are processes occurring simultaneously in the landscape (also suggested by Brondizio et al. 2009), but with their relative importance changing over time. While in the early 90's expansion was predominant across the study area, after 2000 agricultural intensification is prevailing. These processes were shown to be strongly associated with land accessibility, which constrains the expansion of swiddens and encourages intensification. Given the widespread trend of riverine populations to concentrate in villages (Parry et al. 2010a), the general accessibility constrains in the riverine context (Salonen et al. 2012), and the increasing market demand for *farinha*, intensification of swidden cultivation is likely to become a reality far and wide in riverine Amazon. Increasing market opportunities for secondary-forest products could motivate longer fallow periods and increase the sustainability of swidden cultivation in riverine Amazon.

ACKNOWLEDGEMENTS

We thank all the farmers who authorized and contributed to this research. We also thank Luke Parry for contributing information on the location and size of villages of the study area, and Patrick Jansen for assistance with statistical analysis. This research was funded by The Netherlands Fellowship Program (NFP-NUFFIC). The first author also received scholarships from Wageningen University (NL) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (BR) through the Instituto Nacional de Serviços Ambientais da Amazônia – SERVAMB. L.P.D. and M.P.C. received funding from the European Union Seventh Framework Programme (FP7/2007-2013) under grant agreement Number 283093 - The Role Of Biodiversity In climate change mitigatioN (ROBIN). F.B. acknowledges the PARTNERS Research Coordination Network and the grant received from the US National Science Foundation for the Coupled Human and Natural Systems Program (CNH-RSN 1313788). This research is in accordance with the Brazilian regulation on ethics in research, under project number 20361713.7.0000.0006, approved by the Comissão Nacional de Ética em Pesquisa-CONEP and Comitê de Ética em Pesquisa from the Instituto Nacional de Pesquisas da Amazônia (Br).

APPENDIX 2

Table A2.1. Results of the mixed model effects for age of secondary forests and number of past clear-cut events occurred up to 2013. In both models, villages are included as random effects. The values of the slope (β) and its standard error (SE), the degrees of freedom (DF), t-value and P-value for each variable are provided. For the dummy variable settlement size, large villages are taken by the model as the reference category.

Dependent variable	Independent variables	β (SE)		DF	*t-value*	*P-value*
Age of secondary forests						
	(Intercept)	5.59	(0.75)	2198	7.42	< 0.001
	distance to settlement	-0.00	(0.00)	2198	2.75	0.005
	isolated household	4.20	(0.93)	18	4.47	< 0.001
	medium village	1.09	(0.94)	18	1.15	0.265
	small village	0.72	(0.89)	18	0.81	0.431
Number of clear-cut events						
	(Intercept)	2.86	(0.18)	2198	15.32	< 0.001
	distance to settlement	-0.00	(0.00)	2198	-5.88	< 0.001
	isolated household	-0.41	(0.23)	18	-1.79	0.089
	medium village	-0.08	(0.23)	18	-0.35	0.727
	small village	-0.06	(0.22)	18	-0.27	0.789

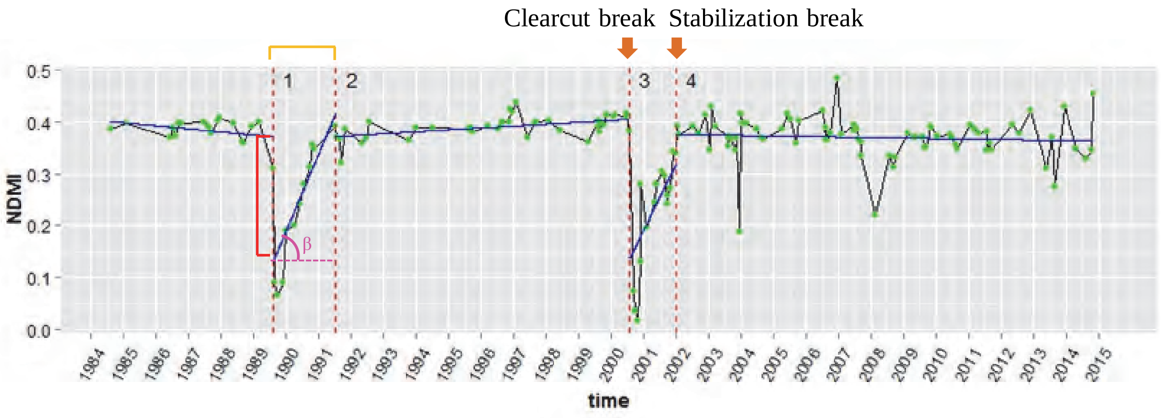

Figure A2.1. Example of a temporal profile spanning from 1984 to 2014, and parameters used for land use change detection. Temporal profile is built from the satellite image observations (green dots) through time. Abrupt changes in NDMI are identified as a breakpoints (red-dashed lines), which separates two segments (blue lines represent the best linear model fitted for each segment). Segments are characterized by their duration (yellow solid line), magnitude (red solid line) and slope (β). The two classes of breakpoints are indicated: clear-cut break (1 and 3) and stabilization break (2 and 4).

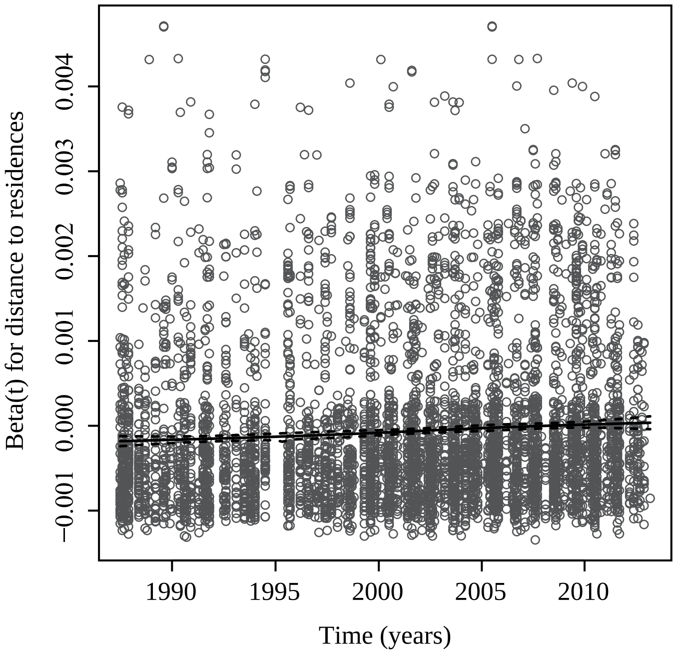

Figure A2.2. Schoenfeld residuals of the relation between hazard rate and distance to settlements (black dots), including village size as a strata. Beta values diverging from zero indicate a change in hazard rate through time. Positive beta values indicate increased hazard rate, i.e. increased probability of a fallow been cut.

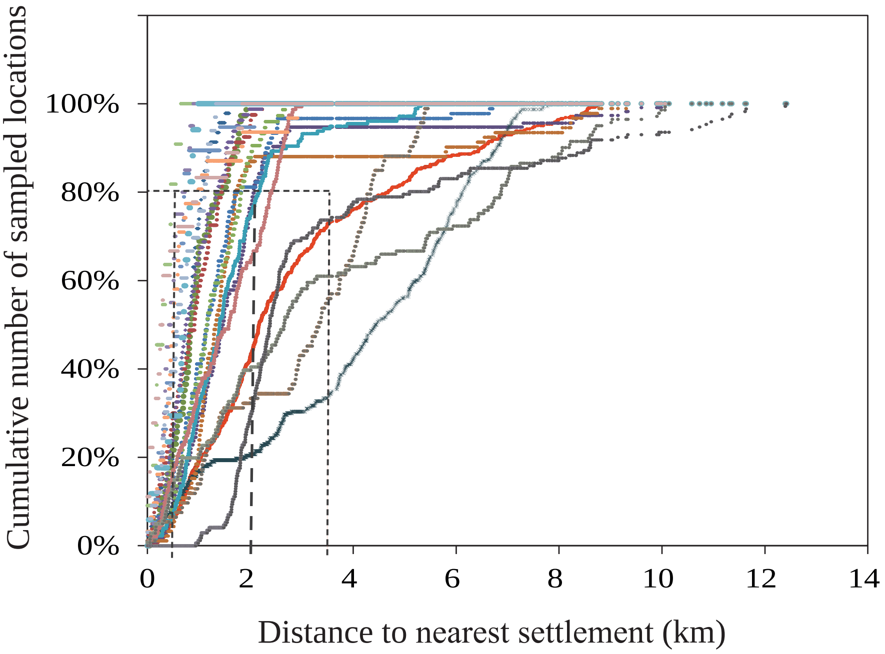

Figure A2.3. Cumulative number of sampled locations at different distances to settlements, for 22 settlements represented by different colours. Black dashed lines indicate average and standard deviation of the distance containing 80% of the sampled locations (2.06 ± 1.65 km; Mean ± SD).

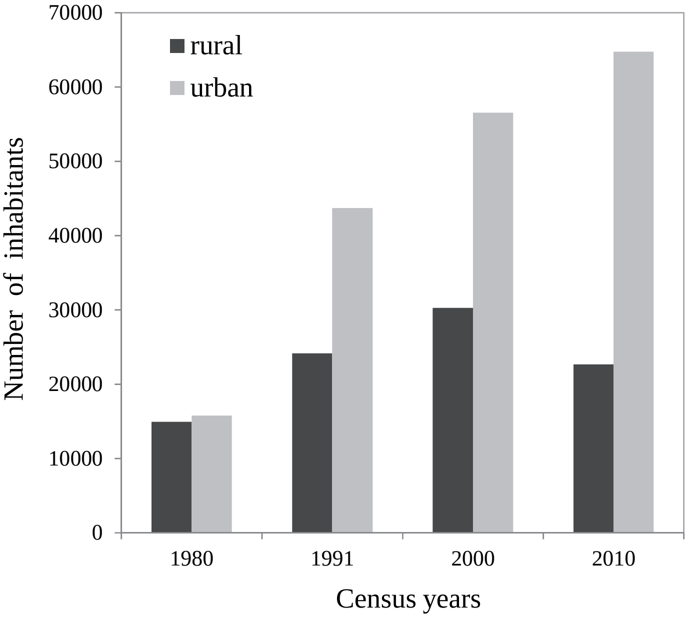

Figure A2.4. Rural and urban population of the three municipalities (Tefé, Alvarães and Uarini) estimated by the national census of 1980, 1991, 2000 and 2010 (IBGE, 2013). In 1980, the three municipalities belonged to the municipality of Tefé. Therefore, for comparison we show the estimated population of the three municipalities together, in the four censuses.

Chapter 3

Loss of secondary-forest resilience by land-use intensification in the Amazon

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Published in Journal of Ecology (2015) 103: 67-77
Special feature: Forest resilience, tipping points and global change processes

ABSTRACT

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 (SF). We assessed resilience as the recovery level of forest structure and species diversity achieved by SF five years after abandonment. We used as a reference the recovery level achieved by SF subjected to the lowest intensity of use, given that these SF 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 SF 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 SF that develop during the fallow period. Land use intensification reduces the resilience of SF 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: Determinants of plant community diversity and structure, secondary succession, swidden agriculture, diversity, fire, legacies, resprout, landscape, soil, Brazil.

INTRODUCTION

Land use and land cover changes are the most important drivers of current global change. Understanding how resilient ecosystems 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 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 (SF), 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 et al. 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 and 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 secondary-forests.

SF are gaining increasing importance in the tropics. In the Brazilian Amazon, 21% of the deforested areas until 2007 regrew to SF, which are currently estimated to cover an area of ca. 150,000 km^2 (Almeida et al. 2010, Embrapa and Inpe 2011). Located along the so-called arc of deforestation and the main rivers, most of these SF 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 and Greenland 1960, Coomes et al. 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 one to two years after abandonment, fallows already achieve a forest structure dominated by trees (Uhl et al. 1981), constituting early-secondary forests. SF 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). SF also provide a wide range of products to local people such as timber, firewood, fruits and fibres (Denevan and Padoch 1987, Chazdon and Coe 1999, Junqueira et al. 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 et al. 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 et al. 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 (two-year cropping of manioc).

Increased land use intensity modifies the landscape configuration by increasing the area covered by young SF and cropping fields (Lawrence et al. 1998, Metzger 2002, Robiglio and 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 et al. 1996, Lawrence et al. 2007, Runyan et al. 2012).

Studies in other tropical regions have reported decreases in biomass accumulation rate (Lawrence et al. 2010), shifts in species composition (Lawrence 2005b) and higher dominance by invasive species (Schneider and Fernando 2010) in SF, 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 and 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 and Jordan 1984, Peña-Claros

2003, Gehring et al. 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 (Figure A3.1).

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 SF that have been subjected to the minimum land use intensity, i.e. SF 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 SF would represent a change in the resilience of SF. Given the importance of initial colonization in determining further successional pathways (Finegan 1996, Guariguata and Ostertag 2001) and the increasing extent of young SF in agricultural landscapes (Metzger 2002, van Breugel et al. 2013), we focused on the first five years of forest succession.

We hypothesized that land use intensification leads to a decrease in the resilience of SF through changes in management intensity, soil quality, and landscape configuration (Figure A3.1). 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.

MATERIAL 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 (Figure A3.2). We sampled 38 early-secondary forests (SF) in 5 communities, named Agrovila (10

SF), Nogueira (11 SF), Vila Sião (6 SF), São Francisco (6 SF) and São Sebastião (5 SF). Villages were located along the black-water Tefé river and tributaries (Figure A3.2), 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 to 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 two years, with only one manioc harvest per cycle.

Data collection and analyses

We sampled 38 SF distributed along land use intensity gradients in each village. We sampled only SF 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 SF within one age class for several reasons. First we were interested in investigating the other possible factors affecting SF 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, landscape configuration and recorded its geographical location.

We selected SF 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 SF 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 (DBH) > 5 cm in 10 x 50 m (canopy size class), individuals with 1 cm < DBH< 5 cm in 5 x 50 m (understorey size class), and individuals with DBH < 1 cm and ≥1 m height in 3 x 50 m (sapling size class). For canopy and understorey size classes we measured DBH 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 densiometer (Lemon 1956), taking 6 measurements per transect. We took measurements every 10 m, along the central line of the 10 x 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, 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 and 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 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 3.1). 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 and 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 (m^2 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, 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 to 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 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 (% resprout, % 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 A3.2). 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 SF had a mean age after abandonment of 5.0 ± 0.1 (SE), were subjected to different management intensities (Figure 3.1a), 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 3.1).

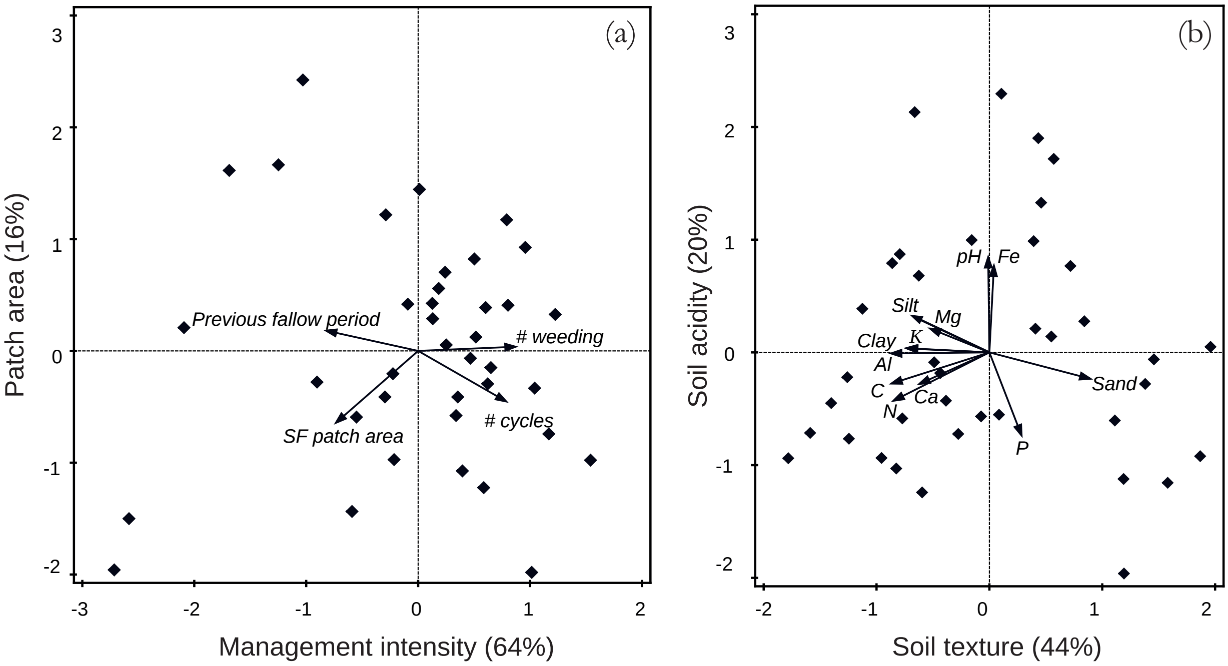

Figure 3.1. Management intensity and soil quality descriptors of early-secondary forests in Central Amazon, Brazil. Principal component analyses (PCA) of the 38 sampled secondary forests near Tefé, Central Amazon, Brazil, using (a) previous fallow period, number of weeding events (# weeding), number of previous swidden-cycles (# cycles), current secondary forest patch area (SF patch area); (b) soil texture and chemical characteristics (Table 3.1). Percentage of variation explained by each axis is provided. Dots represent the 38 sampled secondary forests. 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.

The first two axes of the management intensity PCA explained 80% of the variation in the data (Figure 3.1a). The first axis was significantly correlated to all descriptors of management (Table 3.1): 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 to 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.

Table 3.1. General characteristics of 38 early-secondary forest patches in Central Amazon, Brazil. Mean, standard deviation (SD), 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 (see also Figure 3.1). 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**	
	Explained variation by PCA (%)					**64.0**	
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_2O)	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**
	Explained variation by PCA (%)					**43.8**	**19.7**
Landscape configuration	Linear distance to the forest (m)	506.8	443.8	0	1753	-	-
	Area of forest within 500 m radius (ha)	10.9	17.8	0	78.5	-	-

*$P \le 0.05$, **$P \le 0.01$

Soils had in general low fertility, low pH, low P availability, and high aluminium content (Table 3.1). 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

(Figure 3.1b). The second axis explained 20% of the variation and was positively correlated to pH and Fe and negatively to P (Table 3.1). 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 to the management intensity axis nor to the area covered by old-growth forest (see Table A3.1 in Supporting information). The area covered by old-growth forest was significantly correlated to the management intensity axis (Pearson correlation, $R= -0.65$, $P<0.001$, n=38) (Table A3.1).

Table 3.2. 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	3,868	6,260	27,233
	Density of ramets (stems ha^{-1})	16,861	6,103	8,340	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	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

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 3.3): percentage of resprouting individuals, liana infestation and density of ramets increased with management intensity, while stand basal area and canopy height decreased (Figure 3.2). By increasing management intensity, SF increasingly deviated from the recovery level achieved by same-aged SF subjected to the lowest intensity of use (Figure 3.2). Moving one unit on the management intensity axis (Figure 3.2), basal area decreased 2.9 m^2/ha, canopy height decreased 1.4 m, stems density increased in 2,959 stems/ha, resprouters increased in 15% and liana infestation increased in 8% (Table A3.3, Figures 3.2 and 3.3). Only two forest structure variables were affected by soil characteristics, at a marginal significance level (Table 3.3). Density of genets was negatively related to the soil texture axis, increasing with clay content (Table 3.3 and Figure 3.1b). Canopy openness was positively related to soil acidity axis, increasing with soil pH (Table 3.3 and Figure 3.1b).

The species richness and diversity indices achieved by SF five years after abandonment significantly increased with area of surrounding old-growth forest (Table 3.3). Within five years of succession, SF immediately surrounded by old-growth forest achieved 30% more species (ca. 25 species, based on rarefied richness) than SF without surrounding forest (Figure 3.3, Table A3.3). Inverse Simpson diversity also slightly increased with management intensity (Table 3.3). Species richness, rarefied richness and Shannon diversity were also affected by soil acidity axis, decreasing with soil pH (Figure 3.3). The effect size of soil on the recovery level achieved by SF, in terms of structure and diversity, was always lower than the effects of management intensity and area of surrounding forest (Figure 3.4).

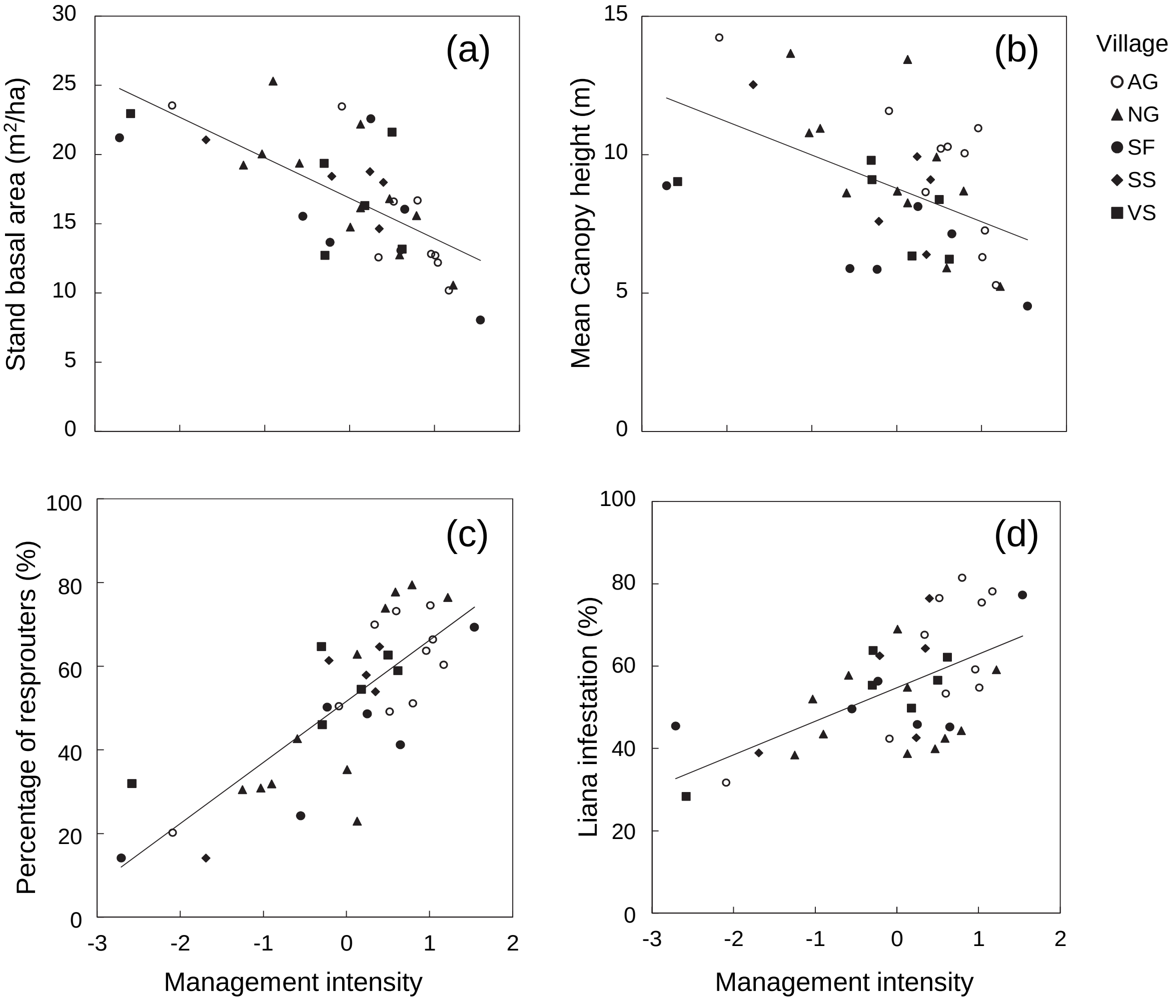

Figure 3.2. The effect of management intensity on structural parameters in secondary forests in Central Amazon, Brazil. (a) Stand basal area, (b) mean canopy height, (c) percentage of resprouters and (d) percentage of liana infestation on trees as a function of management intensity. Management intensity here is represented by the scores extracted from the first axis of the management intensity PCA (Figure 3.1a). 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 (Figure 3.1a). Symbols indicate the secondary forests belonging to the different villages: Agrovila (AG), Nogueira (NG), São Francisco (SF), São Sebastião (SS) and Vila Sião (VS).

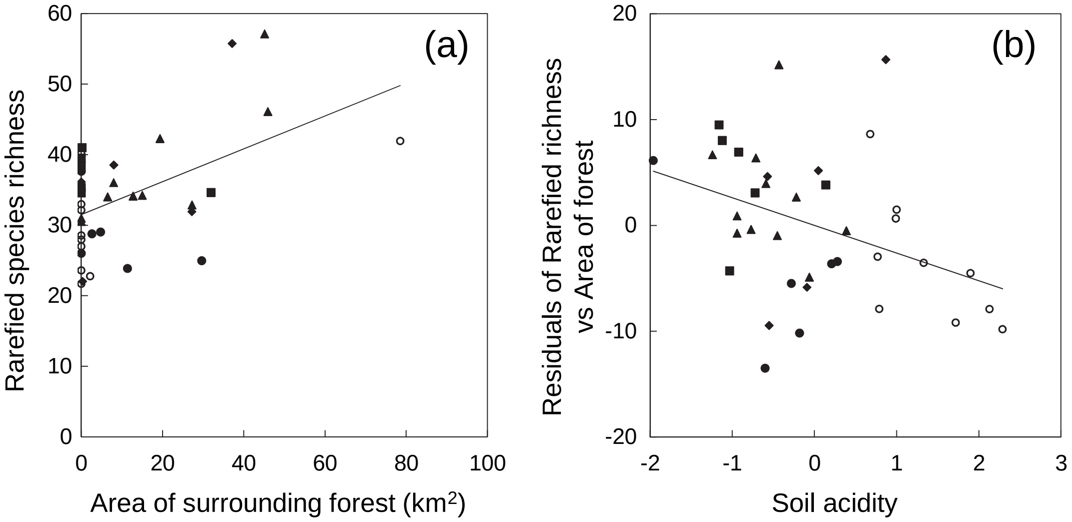

Figure 3.3. Effect of area of surrounding forest and soil acidity on species richness of secondary forests in Central Amazon, Brazil. (a) Relationships between rarefied richness to 150 individuals (Rarefied species richness) and the area of surrounding old-growth forest within 500 m radius of each secondary 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, Figure 3.1b).

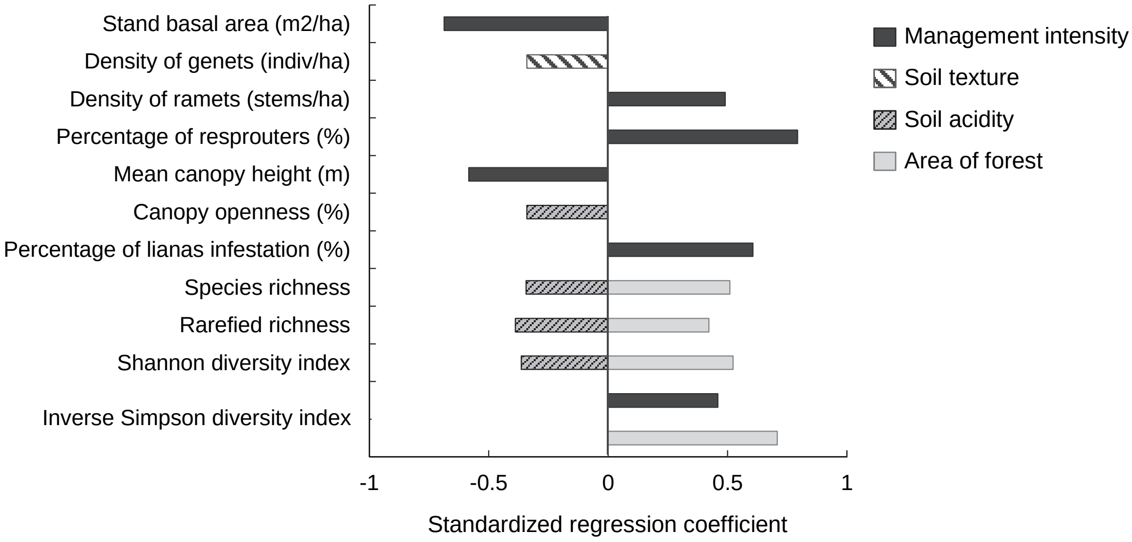

Figure 3.4. Effect size of the explanatory variables on vegetation structure and species diversity of early-secondary forests in Central Amazon, Brazil. Standardized regression coefficients estimated by linear mixed-effects models of vegetation structure and species diversity as a function of management intensity axis (Figure 3.1a), soil texture axis, soil acidity axis (Figure 3.1b) 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 A3.3 for more information).

Table 3.3. 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 (Management 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 (df) of the final model are provided

Response variables			**Management intensity**		**Soil texture**		**Soil acidity**		**Area of forest**	
		df	t	*P*	t	*P*	t	*P*	t	*P*
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

DISCUSSION

In this study we assessed the effect of intensification of swidden cultivation on the resilience of SF 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 (Figure 3.4).

The effect of management intensity on forest resilience

Intensified management practices lead to a steep decrease in the forest structure level achieved by SF five years after abandonment. Our findings demonstrate the -many times overlooked- importance of management practices in determining the structure of SF and indicate an 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 3.3). 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 and 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 and 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 and 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 et al. 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 (Figure 3.2). Therefore, the shift we observed from a seed-dependent towards a sprout-dependent regeneration mechanism with increasing management intensity (Figure 3.2), determines the structure of SF stands. Lawrence (2005a) 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 and Midgley 2001), and as the increase in species richness and diversity throughout secondary succession strongly depend 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 (Figure 3.4). 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* (eg. *V. cayannensis*, *V. gracilis*) dominated the intensively used SF in our study site (*data not shown*). *Vismia* spp also dominate post-pasture SF in Central Amazon (Mesquita et al. 2001), forming large patches of clonal individuals (R.C.G. Mesquita, *unpublished 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 3.3). 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 less than three years (Finegan 1996). Under low intensity of use, 5 years SF had around 30% of trees supporting lianas, but with increasing management intensity this proportion reached up to 80% (Figure 3.2d). 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 SF, as lianas compete both above-ground for light and below-ground for water and nutrients (Schnitzer et al. 2005, Schnitzer and Carson 2010). Therefore, extreme liana infestation levels, such as those we observed in the more intensively managed fields (Figure 3.2d), 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 SF in terms of forest structure and diversity (Table 3.3). This conclusion seems in contrast to studies that showed a decrease in soil quality with land use intensification (Lawrence et al. 2007, Runyan et al. 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 A3.2) and pH (R = 0.48, P = 0.003; Table A3.2) suggest effects of land use intensification on soil properties (Table A3.2). 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 A3.2) might also be a consequence of burning that recurrently adds ash to the soil surface (Nye and Greenland 1960, Certini 2005). Additionally, the negative correlation between available P and pH (R= -0.60, P< 0.001, Table A3.1), 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 (Figure 3.4).

A progressive loss of phosphorus availability with increasing number of swidden cycles has been related to the decreased rate of fallow regrowth (Runyan et al. 2012). However, those studies reported P levels at least 3 times higher than what this (Table 3.2) 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 3.1), and was not related to forest structure (Table A3.2). 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 et al. 1996, Silva-Forsberg and 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 SF (Table 3.3, Table A3.3 and Figure 3.3). This is probably due to a reduced propagule dispersal probability with increasing distance from the source (Helmer 2000, Cubiña and Aide 2001). Not only old-growth forests but also developed SF may act as important sources of diversity. SF patches located closer to the old-growth forest were also surrounded by less intensively used SF (Table A3.2), 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 (Figure A3.2). Given that species accumulate through time in successional forests (Finegan 1996), we can expect species richness and diversity to increasingly deviate in SF 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 (Figures 3.2 and 3.3) 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 et al. 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) (Figure A3.3), showing ever lower recovery rates (Figures 3.2 and 3.3). 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 SF to approach a successional pathway achieved under less intensified conditions. Although our methodology did not allow us to evaluate how those SF will develop over time, chronosequence and monitoring studies in the Central Amazon found low recovery rates and seedling growth in SF 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. 2014). Therefore, it is likely that strong intensification of swidden cultivation will also push SF into an arrested successional state, comparable to those found in abandoned pastures.

Implications

The current intensification of swidden cultivation systems may have important socioeconomic consequences. One such consequence is the reduction of crop productivity (Arnason 1982, Silva-Forsberg and 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 SF 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, secondary forests 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.

ACKNOWLEDGMENTS

The authors are grateful to the inhabitants of the villages Vila Sião, São Francisco, São Sebastião, Nogueira and Agrovila, for authorizing and contributing to this research. We are grateful to Reney, Francisco and Rosa Falcão for assistance during field work. We also thank the Instituto Chico Mendes de Conservação da Biodiversidade for authorizing research in the National Forest Reserve FLONA Tefé and for logistic assistance in the field. This research was funded by The Netherlands Fellowship Program (NFP-NUFFIC). A.C.C.J. received scholarships from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (Br) and Wageningen University (NL)

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

APPENDIX 3

Table A3.1. Pearson correlation among predictors included in the linear mixed-effects model. Correlation coefficients (Pearson's R) among the first axis of the Principal component analysis (PCA) using descriptors of management intensity (Management intensity), soil PCA first axis (Soil texture), soil PCA second axis (Soil acidity) and the area of surrounding old-growth forest in a 500 m radius (Area of forest). Data from 38 early-secondary forests in Central Amazon, Brazil.

	Management intensity	Soil texture	Soil acidity	Area of forest
Management intensity	1			
Soil texture	0.25	1		
Soil acidity	0.19	0	1	
Area of forest	- 0.65**	-0.27	-0.07	1

**$P \leq 0.01$

Table A3.2. Pearson correlation among all individual variables measured in 38 early-secondary forests in central Amazon, Brazil. Correlation coefficients area provided, and significance levels are indicated as underlined for α < 0.05 are underlined and bold for α < 0.0018 (Bonferroni correction applied).

		Structure							Diversity				Management intensity				Soil properties											
		Stand basal area (m2/ha)	Density of genets (indiv/ha)	Density of ramets (stems/ha)	Percentage of resprouters (%)	Mean canopy height (m)	Canopy openness (%)	Lianas infestation (%)	Richness	Richness (rarefied)	Shannon diversity	Inverse Simpson diversity	Number of swidden cycles	Mean number of weedings	Previous fallow age	Secondary forest patch area	Percentage of clay (%)	Percentage of silt (%)	Percentage of sand (%)	pH (H2O)	Al (cmol/dm3)	C (g/kg)	Ca (cmol/dm3)	K (cmol/dm3)	Mg (cmol/dm3)	N (g/kg)	Fe (mg/dm3)	P (cmol/dm3)
Structure	Stand basal area (m2/ha)	1																										
	Density of genets (indiv/ha)	-0.22	1																									
	Density of ramets (stems/ha)	**0.57**	**0.72**	1																								
	Percentage of resprouters (%)	**-0.60**	0.13	**0.64**	1																							
	Mean canopy height (m)	**0.68**	-0.04	-0.41	-0.46	1																						
	Canopy openness (%)	-0.03	-0.37	-0.33	0.00	-0.42	1																					
	Lianas infestation (%)	**-0.61**	-0.14	0.15	0.41	-0.45	0.09	1																				
Diversity	Richness (number of species)	0.31	0.02	-0.30	**-0.41**	0.37	-0.16	-0.32	1																			
	Richness (rarefied)	0.24	-0.34	**-0.44**	-0.32	0.26	-0.04	-0.16	**0.91**	1																		
	Shannon diversity	0.10	-0.15	-0.17	-0.18	0.18	-0.17	-0.16	**0.76**	**0.85**	1																	
	Inverse Simpson diversity	-0.03	-0.16	-0.14	-0.16	0.13	-0.14	-0.04	**0.66**	**0.76**	**0.88**	1																
Management intensity	Number of fallow cycles	**-0.77**	0.22	**0.61**	**0.74**	**-0.54**	0.09	**0.57**	-0.41	-0.34	-0.22	-0.07	1															
	Mean number of weedings	**-0.51**	0.05	0.42	**0.64**	-0.31	-0.01	0.46	-0.48	-0.37	-0.17	-0.08	**0.58**	1														
	Previous fallow age	0.44	0.02	-0.44	**-0.66**	0.49	-0.14	**-0.51**	**0.51**	0.35	0.16	0.21	**-0.55**	**-0.60**	1													
	Secondary forest patch area	0.48	0.05	-0.28	-0.49	0.09	0.25	-0.40	-0.05	-0.20	-0.36	-0.36	-0.37	**-0.56**	0.45	1												
Soil properties	Percentage of clay (%)	0.43	0.19	-0.15	-0.45	**0.55**	-0.37	-0.44	0.33	0.18	0.10	0.00	-0.44	-0.40	0.31	0.18	1											
	Percentage of silt (%)	0.22	0.32	0.10	0.06	0.35	-0.23	-0.01	0.02	-0.14	-0.07	-0.02	-0.03	0.11	-0.02	-0.14	0.24	1										
	Percentage of sand (%)	-0.40	-0.34	0.02	0.21	**-0.56**	0.35	0.26	-0.20	0.00	-0.01	0.02	0.27	0.14	-0.17	-0.01	**-0.71**	**-0.85**	1									
	pH (H2O)	-0.36	0.42	**0.59**	0.43	0.03	**-0.55**	0.14	-0.31	-0.39	-0.28	-0.13	0.48	0.22	-0.21	-0.15	-0.04	0.15	-0.07	1								
	Al (cmol/dm3)	0.37	0.28	-0.03	-0.22	**0.55**	-0.45	-0.35	0.41	0.20	0.14	0.04	-0.32	-0.20	0.30	0.05	**0.74**	**0.58**	**-0.82**	-0.05	1							
	C (g/kg)	0.21	0.32	0.13	-0.03	0.37	-0.28	-0.17	0.41	0.25	0.27	0.24	-0.18	0.00	0.09	-0.11	0.41	**0.56**	**-0.64**	-0.12	**0.70**	1						
	Ca (cmol/dm3)	0.27	0.18	-0.10	-0.30	0.39	-0.13	-0.23	**0.68**	**0.55**	0.48	**0.50**	-0.27	-0.43	0.28	0.01	0.42	0.17	-0.35	-0.11	0.38	**0.60**	1					
	K (cmol/dm3)	0.03	0.47	0.31	0.00	0.21	-0.45	-0.05	0.26	0.06	0.11	0.11	-0.10	-0.16	0.10	-0.05	0.38	0.45	**-0.52**	0.23	**0.50**	**0.76**	**0.52**	1				
	Mg (cmol/dm3)	0.13	0.35	0.07	-0.21	0.25	-0.03	-0.22	0.04	-0.17	-0.31	-0.21	-0.12	-0.26	0.32	0.26	0.37	0.27	-0.40	0.21	0.25	0.29	0.31	**0.55**	1			
	N (g/kg)	0.23	0.19	-0.03	-0.16	0.34	-0.11	-0.27	0.45	0.31	0.30	0.24	-0.25	-0.08	0.19	-0.07	**0.55**	0.44	**-0.63**	-0.34	**0.75**	**0.90**	**0.59**	**0.59**	0.29	1		
	Fe (mg/dm3)	-0.14	-0.06	-0.04	0.01	0.12	-0.37	0.28	-0.22	-0.14	-0.13	-0.03	0.11	0.04	-0.05	-0.25	-0.10	0.29	-0.14	**0.50**	-0.05	-0.22	-0.17	0.07	0.10	-0.31	1	
	P (cmol/dm3)	-0.11	-0.35	-0.23	0.09	-0.42	**0.58**	0.09	0.05	0.18	0.09	-0.01	0.00	-0.11	-0.07	0.02	-0.38	-0.29	0.41	**-0.61**	-0.29	-0.02	-0.04	-0.12	-0.14	0.05	-0.33	1
Landscape configuration	Area of forest (ha)	0.42	-0.12	-0.39	**-0.60**	0.43	-0.17	-0.48	**0.60**	**0.51**	0.38	0.19	**-0.52**	**-0.56**	**0.67**	0.31	0.42	0.02	-0.25	-0.13	0.37	0.14	0.35	0.00	0.03	0.19	-0.97	-0.20

Table A3.3. Non-standardized effect size of the explanatory variables on vegetation structure and species diversity of early-secondary forests in Central Amazon, Brazil. Non-standardized regression coefficients estimated by linear mixed-effects models of vegetation structure and species diversity as a function of management intensity axis (Figure 3.1a), soil texture axis, soil acidity axis (Figure 3.1b) and area of surrounding old-growth forest within 500 m radius of each secondary forest patch (Area of forest). Regression coefficients (coef.) and corresponding standard errors (SE) are given on the original scales of the variables. Only significant effects are included based on the final models reported on Table 3.3.

	Response variables	**Managemenent intensity**		**Soil texture**		**Soil acidity**		**Area of forest**	
		coef.	**SE**	**coef.**	**SE**	**coef.**	**SE**	**coef.**	**SE**
Structure	Stand basal area (m^2ha^{-1})	-2.92	0.51						
	Density of genets (indiv ha^{-1})			-1021.29	652.50				
	Density of ramets (stems ha^{-1})	2959.24	774.90						
	Percentage of resprouters (%)	14.62	1.89						
	Mean canopy height (m)	-1.41	0.31						
	Canopy openness (%)					-0.02	0.01		
	Percentage of lianas infestation (%)	8.03	1.81						
Diversity	Species richness					-2.81	1.64	0.32	0.07
	Rarefied richness					-2.54	1.35	0.22	0.06
	Shannon diversity index					-0.15	0.07	0.01	0.00
	Inverse Simpson diversity index	2.65	1.06					0.23	0.06

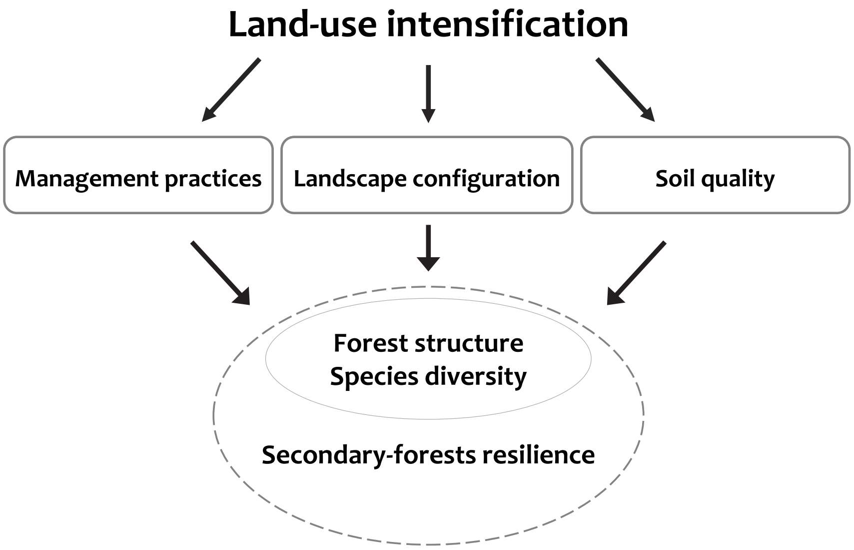

Figure A3.1. Conceptual framework on how land use intensification affects secondary-forests resilience.

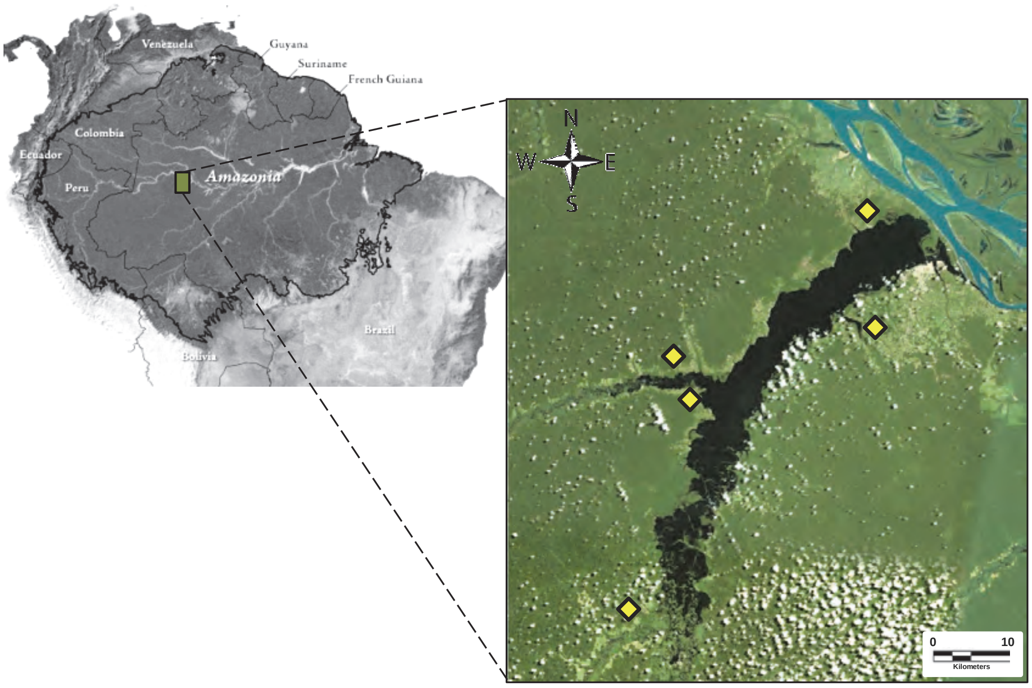

Figure A3.2. Map of the study area**.** To the left, map of the Amazon region indicating the location of the study area, at the municipality of Tefé, Amazonas State, Brazil. To the right, satellite image of the study area showing Rio Tefé at the centre (in black colour) and Rio Amazonas at the top right (in blue colour). Old-growth forest is shown in dark green and secondary forests in light green colours, cities and bare soils are shown in light grey; white dots dispersed around are clouds. The five villages where secondary forests were sampled are indicated with yellow diamonds.

Figure A3.3. Diagram of the effects of land use intensity on the structure of secondary forests in central Amazon, Brazil. To the left two pictures of secondary forests (SF) subjected to low intensity of use: one swidden cycle (2 yrs period) after old-growth forest was slashed, agricultural field was weeded only once. To the right two pictures of SF subjected to high intensity of use: more than eight swidden cycles, agricultural fields weeded 2-4 times per cycle, followed by a mean fallow period of four years. All SF represented here were abandoned from agriculture 5-6 years ago. Triangles at the bottom indicate the direction of change in four forest structure variables along a gradient of land use intensity.

Chapter 4

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

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Submitted for publication

ABSTRACT

Secondary succession in the tropics can follow divergent pathways. Land-use history can lead to alternative successional communities with distinct floristic composition, which may never converge. The mechanisms underlying the effects of land use on succession are still unclear.

Here we investigate how land-use shapes species composition by evaluating the relative roles of changes in management practices, soil properties and landscape configuration, which have rarely been jointly assessed. We investigated whether land use acts as a filter for species composition and tested three hypotheses: (1) that there are specific species assemblages associated with different land-use intensities, (2) that the sprouting ability of these species helps explaining species-environment relations and (3) that increasing land-use intensity leads to a decrease in alpha and beta-diversity of the regrowing communities.

We find that land-use intensity determines species composition through hierarchical effects of management practices and soil properties. With increasing land use intensity, management practices of cutting and burning filters out seed-dependent species and selects for strong sprouters. Further on, decreased soil quality determines the species that will establish and dominate the community. As a consequence of these local filters, species diversity decreases and early-communities become more similar to each other.

Species composition of successional forests is strongly determined by different land use intensities. Filtering effects of management practices and soil quality narrow down the range of species by selecting for persistence over regeneration strategies. We identified species assemblages associated with different levels of land-use intensity that are characterized by their canopy dominant species.

Synthesis: Land use history is known to engender divergent successional communities, but the underlying mechanisms driving and sustaining divergence remain unclear. This study enlightens such mechanisms showing that management intensity and soil quality determine species composition through filtering effects acting early in succession. Therefore, accounting for detailed land-use history is necessary to improve the understanding of tropical secondary succession. We present a list of indicator species for different levels of past land-use intensity in the Amazon.

KEYWORDS: *Cecropia*, Brazil, fire, legacies, phosphorus, slash and burn, soil, sprouting, succession, *Vismia*

INTRODUCTION

Under the current high rates of land cover change in the tropics, secondary forests expand in area and become more important in the biodiversity conservation and ecosystem services agendas. Studies have shown, however, that secondary forests do not form a homogeneous category, with regrowth rates and species composition being highly variable across and within sites (Chazdon 2008). 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 and Aide 2001, Robiglio and Sinclair 2011), soil properties (Lawrence 2005b, 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). Although the relative importance may vary in space and time, there is also evidence for a deterministic effect of land use on succession.

Past land-use history has been associated with alternative pathways (Mesquita et al. 2001, Hooper et al. 2004, Suding et al. 2004) that may not converge during succession (Norden et al. 2011, Longworth et al. 2014). Abiotic conditions, dispersal limitation, priority effects and species interactions have been evoked to explain such divergent successional pathways (Norden et al. 2011), but mechanisms underlying the effect of land use remain unclear. The broadly-termed "land use effect" is actually mediated by concomitant effects of landscape configuration, management practices and soil properties. Interestingly, these three factors have rarely been jointly assessed (Aragón and Morales 2003, Lawrence 2005b, Robiglio and Sinclair 2011), although disentangling their role is essential to assess 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 strengthen species dispersal limitation (Robiglio and Sinclair 2011, Jakovac et al. 2015) and potentially determine the species able to first colonize and dominate new open sites. In the wet tropics, where agricultural land is mostly managed by slashing and burning practices, the number of cutting and burning events determines vegetation structure and regrowth rate in pasture lands (Zarin et al. 2005) as well as in shifting cultivation (Jakovac et al. 2015). We have shown before that such practices led to an increase in the percentage of resprouting individuals in successional communities (Jakovac et al. 2015). Consequently, by selecting for traits like sprouting ability and fire-resistant seeds, such slash-and-burn practices can induce a shift in species composition (Hooper et al. 2004). Interactively, land use may affect soil conditions by depleting nutrients and changing physical properties (Palm et al. 1996, Lawrence et al. 2007, Runyan et al. 2012). Although the role of soils in structuring communities remains unclear, the distribution of many tropical species depends on nutrient availability (John et al. 2007, Toledo et al. 2012, Condit et al. 2013). These land-use underlying factors 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 disentangle how land-use shapes successional communities testing the hypothesis that changes in species composition are a result of filtering processes imposed by management practices, soil quality and landscape configuration. We focused on early stages of succession, when a few species dominate the canopy and the effects of land use have not been diluted through successional age. The early species that form the canopy at the first ca. 20 years of succession (Finegan 1996), regulate environmental conditions in the understory (Kabakoff and 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.

We used a novel sampling design where successional age was kept constant across sites (ca. 5 years after abandonment) and sites were located along gradients of land-use intensity. In agricultural landscapes transformed by swidden cultivation in the Amazon, we sampled 38 early-secondary forests that varied in management intensity and soil characteristics and were located at different distances to the old-growth forest. By interviewing local inhabitants we reconstructed a detailed land-use history of each secondary forest surveyed. More specifically, we assessed (i) the roles of management intensity, soil quality and landscape configuration in determining species composition, (ii) whether there were species associated with specific environmental conditions, (iii) what role sprouting ability of those species plays in explaining such relationships and (iv) how alpha- and beta-diversity of early-successional communities change with land-use intensity. Unravelling the processes underlying land-use effects can improve the understanding of how communities are structured during secondary succession.

METHODS

Study site

The study was carried out in the middle Amazonas River, in the municipalities of Tefé and Alvarães, Brazil. The landscape in this region has been mainly transformed by cultivation of cassava in swidden-fallow systems. Agriculture is practiced by smallholder farmers in cropping fields of 1 to 3 ha, and is based on traditional practices that include family and collective labour. Study sites are located on non-flooded areas (*terra firme*) over soils classified as oxisols and ultisols by USDA soil classification and as Acrisol by the World Soils reference database (WRB 2014). Soils are generally acid, with high aluminium content and low bases saturation (Jakovac et al. 2015).

Data collection

We sampled 38 early-secondary forests (SF) in 5 villages, Agrovila (10 SF), Nogueira (11 SF), Vila Sião (6 SF), São Francisco (6 SF) and São Sebastião (5 SF), which were 3 to 66 km apart from each other. 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) years, and were submitted 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 at different villages and searching for variations in this three factors within villages we believe to have covered the variation found in our study landscape. Previous study showed that the variation in soil properties was generally unrelated to management intensity, with the exception of pH that increased (R=0.48, P=0.003) and clay content that decreased (R=-0.44, P=0.006) with number of cycles (Jakovac et al. 2015).

Management intensity was defined by the following practices: number of swidden-fallow cycles, number of weeding events taken during the previous cropping period, age of the previous fallow and the current area of the SF patch. We selected for SF regrowing on sites that had been used for 1 up to 10 swidden-fallow cycles. We assessed the land-use history of every SF by interviewing landowners and their families.

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 carbon, total N, available P [Mehlich-1], K, Ca, Mg, Fe, Al and pH) and texture analysis, following published protocol (EMBRAPA 2011).

Landscape configuration was defined as the area covered by old-growth forest within a 500 m radius surrounding each SF patch (79 ha area). 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 (ESRI 2012). For detailed methodology see Jakovac et al. (2015).

To characterize the 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 diameter at breast height (d.b.h.) ≥ 5 cm in 50 x 10 m transect, and genets 1-5 cm in dbh in 50 x 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 by 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 of an experienced parataxonomist.

Statistical analyses

To evaluate how management intensity, soil properties and landscape configuration shape species composition of early-secondary forests, we applied a multivariate regression tree (MRT) on standardized basal area. We included as environmental variables all descriptors of management practices, soil quality and landscape configuration (De'ath 2002). MRT is a type of constrained cluster analysis that groups samples to minimize differences within groups and maximize differences among groups taking into account both species composition and environmental variables (De'ath 2002). MRT is especially suited for identifying and modelling species-environmental relationships while including high-order interactions (De'ath 2002). We based 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 (De'ath 2002). We then calculated the indicator value for each species at each group formed by the MRT, to evaluate whether species were significantly associated with each group (Dufrene and Legendre 1997). 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 and Legendre 1997).

To evaluate the processes underlying the effect of land use on species composition, we assessed how the groups formed by the MRT differed in terms of percentage of resprouting individuals, percentage of strong-sprouter species and species alpha- and beta-diversity. Percentage of resprouting individuals at each SF was calculated as the proportion of resprouting genets to the total number of genets. We classified the species as strong-sprouter when $\geq$ 60% of its individuals were sprouting over the whole dataset, considering only species with more than 10 individuals sampled. We then calculated the percentage of strong-sprouter species at each SF as the proportion of strong-sprouter species to the total number of species. Alpha diversity was calculated as the total number of species sampled at each SF (500 m^2). Groups were compared using analysis of variance followed by Tukey pairwise comparisons, at a level of significance of 0.05. For count data on alpha-diversity, we tested the differences among groups with a generalized linear model using Poisson distribution.

We assessed beta-diversity as the variability in species composition among SF within each MRT group, also called multivariate dispersion (Anderson et al. 2006). Samples were ordered using a Principal Coordinate Analysis based on Jaccard similarity index. Then, the average distance from each individual sample to its group centroid in the multivariate space was calculated (Anderson et al. 2006). Higher values of this distance indicate higher dispersion of the samples within a group, and therefore, higher beta-diversity. Pairwise comparisons of beta-diversity among MRT groups was performed with a permutation test with 999 permutations.

Analyses were performed using the R-Studio interface to R (Core-Team 2013), using the following packages: *mvpartwrap* for MRT, *indicspecies* for indicator species analysis, and *vegan* (*betadisper* function) for beta-diversity and pairwise comparison. Percentages (resproutings, clay and silt) were transformed by the arcsine of the square root prior to analysis.

RESULTS

We sampled a total of 7,373 individuals belonging to 280 species, 153 genera and 54 families including trees, shrubs and palms with dbh > 1 cm. Half of the species occurred only occasionally, with 138 species being single or doubletons. The most common 23 species were responsible for 80% of the total basal area and were usually the ones at the canopy layer. Most of the species had at least one individual resprouting (178 species), but only 30 species were classified as strong-sprouters.

The MRT analysis indicated number of swidden-fallow cycles, clay content and phosphorus availability in the soil as determinants of species composition (Figure 4.1). The best MRT had four leaves (groups) and explained 35% of species variance. The first split of the MRT was determined by number of swidden-fallow cycles, and accounted for 47% of the species variance explained by the tree. This first split grouped together all six SF that were subjected to only one swidden-fallow cycle (one cycle group -Cy). The second split was determined by clay content in the soil, and explained an additional 28% of the species variance, grouping seven SF located on soils containing ≥22% of clay (high clay group-HC). The final split, which accounted for the remaining 24% of the species variance, was determined by phosphorus availability in the soil. This split grouped together 10 SF located on soils with <0.04 cmol dm^{-3} of available phosphorus (low phosphorus group-LP). The remaining 15 SF were grouped under the relatively high phosphorus group (HP; ≥0.04 cmol dm^{-3}). These four groups of secondary forests represent distinctive associations of species assemblages and environmental conditions (Table 4.1).

The four groups defined by the MRT were characterized by 22 indicator species (Figure 4.1; Table 4.2). From those, 18 species were assigned as indicator due to its higher frequency and abundance in a given group, yet also being found in other groups (Table 4.2). Only four indicator species occurred exclusively in one group, three of them being associated with the one-cycle group (Cy). The Cy group was associated with six indicator species, among which *Cecropia sciadophylla* Mart. (Urticaceae) and *Miconia minutiflora* D.C. (Melastomataceae) had the highest indicator values. *Cecropia sciadophylla* was the dominant species, making 42% of the basal area in this group of secondary forests (Table 4.2). The HC group had *Jacaranda copaia* (Aub.) D. Don (Bignoniaceae), *Solanum schlechtendalianum* Walp. (Solanaceae) and *Vernonia sp.* (Asteraceae) as indicator species. *Jacaranda copaia* was the dominant species, making 32% of the group basal area (Table 4.2). *Solanum* and *Vernonia* had relatively high number of individuals but very low basal area (Table 4.2), as they are typically understory woody shrubs achieving 3 m in height on average. The LP group was associated with 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 4.2). The remaining group (HP) was characterized by eight species, with *Croton palanostigma* Klotzsch. (Euphorbiaceae) and *Tapirira guianensis* Aubl. (Anacardiaceae) as the strongest indicators (Figure 4.1).

Croton palanostigma and *Cassia spruceana* Benth. (Fabaceae) were the dominant species in this group of secondary forests (Table 4.2).

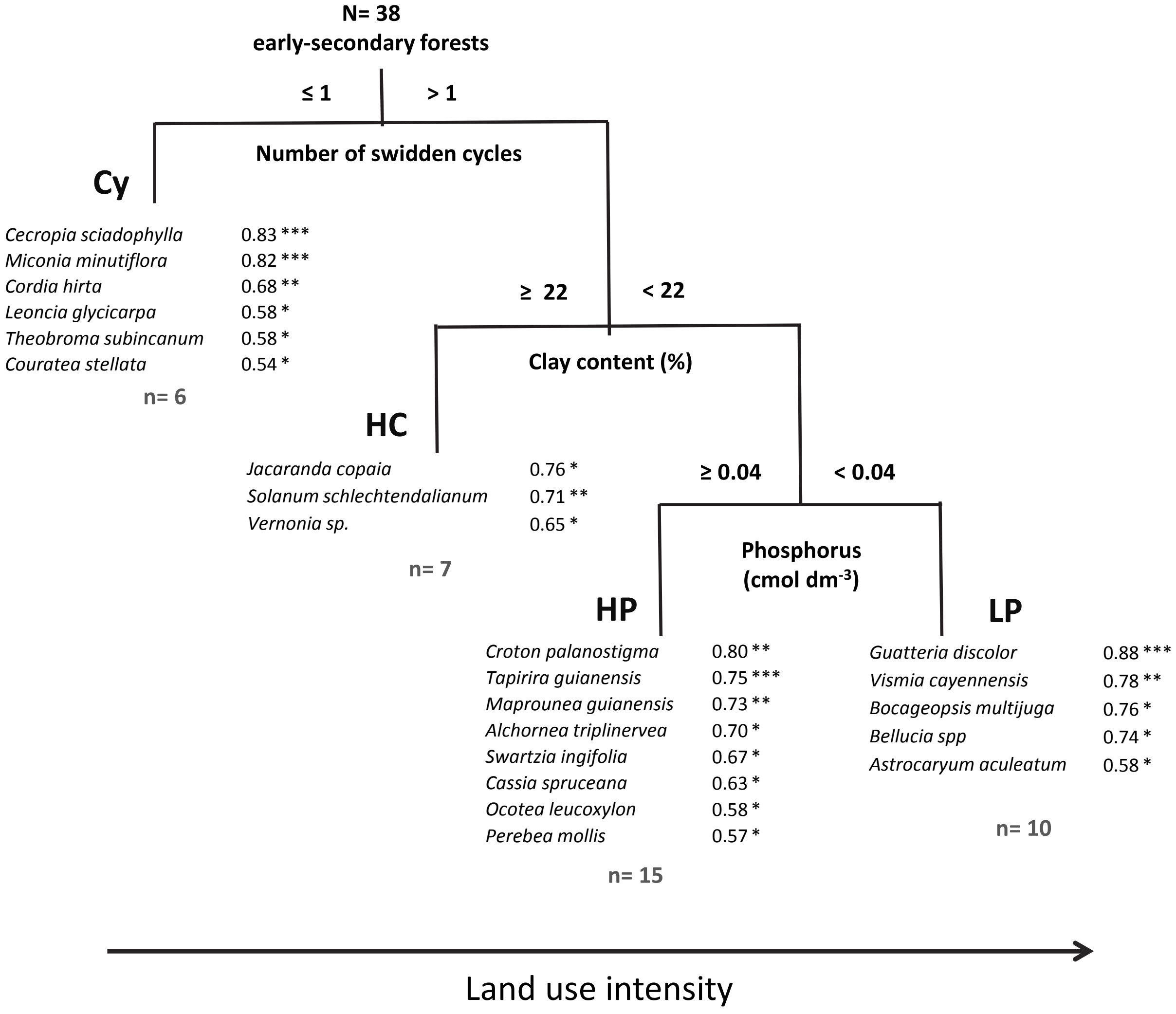

Figure 4.1. Multivariate Regression Tree of species composition of 38 secondary forests in Brazil (total of 280 species). At each "leaf" of the tree, a name to the group is given: Cy - one swidden-cycle; HC - high clay; HP - high phosphorus and LP - low phosphorus. At each leaf all the significant indicator species are listed, followed by their respective indicator value and level of significance (*P<0.05, **P<0.01, ***P<0.001), and the number of secondary forest plots grouped (n).

Table 4.1. Characteristics of the four groups of secondary forests formed by the Multivariate Regression Tree (Figure 4.1). Mean and standard deviation (Mean [SD]) values of the environmental variables are provided (Figure 4.2). MRT groups abbreviation stands for Cy - one swidden-cycle; HC - high clay; HP - high phosphorus and LP - low phosphorus.

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 (years past)	> 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 configuration								
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 (g kg^{-1})	18.41	(3.85)	19.81	(4.54)	17.61	(6.21)	14.60	(3.25)
N (g kg^{-1})	1.51	(0.41)	1.57	(0.23)	1.37	(0.43)	0.99	(0.19)
P (mg dm^{-3})	2.67	(1.21)	2.14	(0.90)	4.40	(1.55)	1.50	(0.53)
K (mg dm^{-3})	0.08	(0.01)	0.08	(0.01)	0.07	(0.02)	0.07	(0.02)
Fe (mg dm^{-3})	267.33	(94.56)	255.57	(68.32)	250.27	(65.13)	345.60	(96.50)
Ca (cmolc dm^{-3})	0.08	(0.02)	0.09	(0.03)	0.06	(0.03)	0.04	(0.01)
Mg (cmolc dm^{-3})	0.19	(0.08)	0.17	(0.02)	0.13	(0.04)	0.14	(0.07)
Al (cmolc dm^{-3})	5.26	(1.54)	4.97	(0.76)	4.15	(1.15)	4.01	(0.69)
CEC (cmolc dm^{-3})	5.63	(1.64)	5.33	(0.83)	4.42	(1.25)	4.27	(0.76)
Sum of bases (cmolc dm^{-3})	0.37	(0.10)	0.35	(0.04)	0.27	(0.08)	0.27	(0.09)

The groups formed by the MRT were significantly different in alpha and beta-diversity as well as in the percentages of resproutings and strong-sprouter species (Figure 4.2). All these parameters showed a consistent trend of change following the MRT grouping. The secondary forests within the Cy group had significantly higher number of species and were more different among each other than secondary forests of the LP group (for alpha diversity: $F_{3,34}$=5.18, P = 0.004; for beta diversity: $F_{3,34}$=4.03, P = 0.015; Figure 4.2a,b). The groups HC and HP had intermediary 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; Figure 4.2c). 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;

Figure 4.2d). Accordingly, the indicator species of the Cy and HC groups showed lower sprouting ability than the species associated with the HP and, specially, to the LP group (Table 4.2).

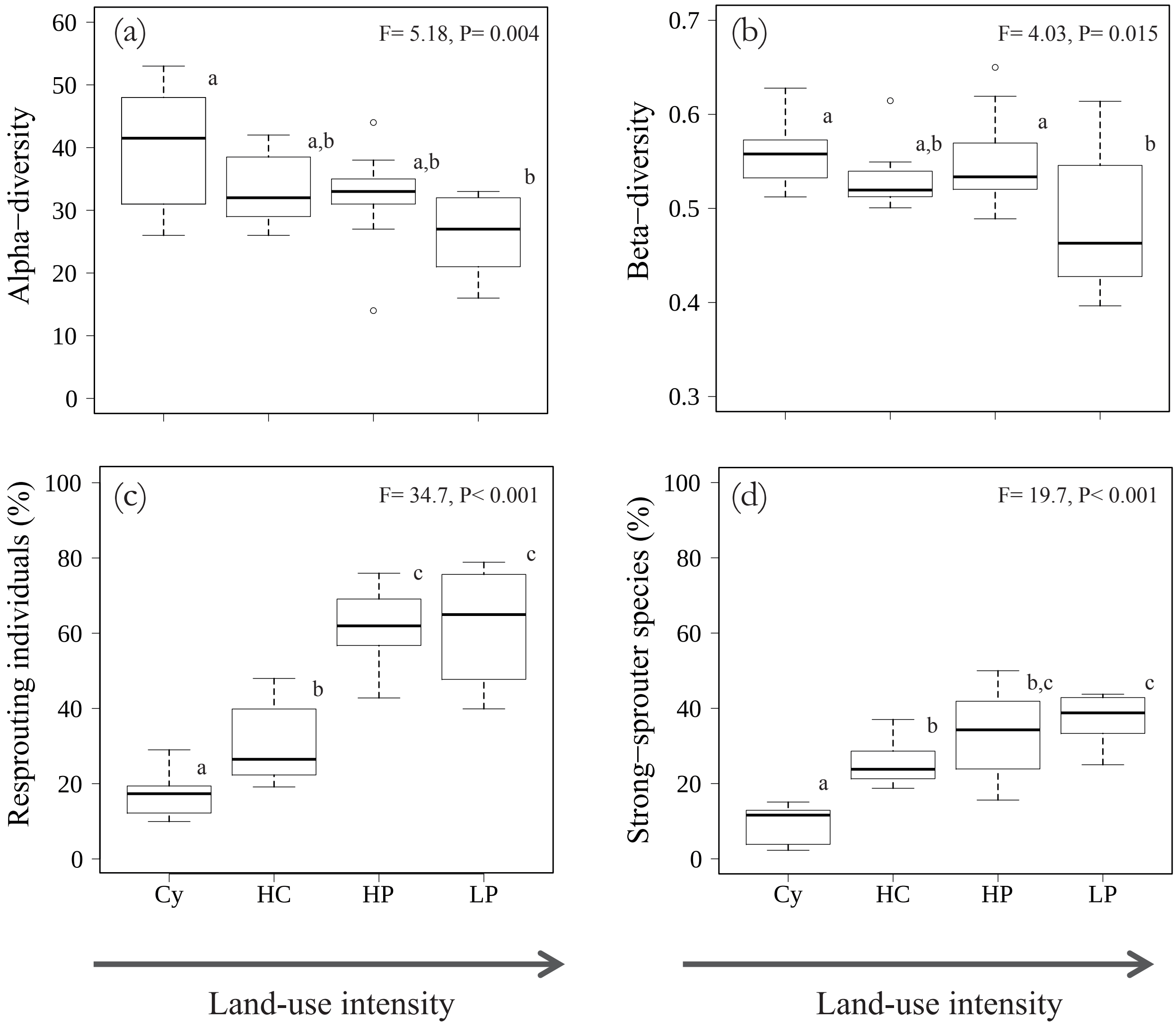

Figure 4.2. Changes in community diversity and regeneration strategies with land use-intensity. Means and standard deviations of (a) alpha-diversity, (b) beta-diversity, (c) percentage of resprouting genets and (d) percentage of strong-sprouter species, for each group formed by the Multivariate Regression Tree. Cy (one cycle), HC (high clay content), HP (high phosphorus content), LP (low phosphorus content). Significant differences among groups are indicated by different letters.

Table 4.2. List of indicator species of the groups formed by the Multivariate Regression Tree (Figure 4.1). For each species, we present the total number of individuals sampled (total genets); the relative basal area at each MRT group (Cy, HC, HP and LP); and the percentage of resprouting genets within the whole dataset (Total) and within each MRT groups (Cy, HC, HP and LP). Values in bold indicate the indicator species-group association. Absence of the species in the sample is represented by (-).

Indicator species	**Total genets**	**Relative basal area (%)**				**Resproutings (%)**				
		Cy	**HC**	**HP**	**LP**	**Total**	**Cy**	**HC**	**HP**	**LP**
One cycle (Cy)										
Cecropia sciadophylla	244	**41.8**	12.7	1.3	0.8	4.5	**4.7**	2.9	-	6.3
Miconia minutiflora	8	**0.4**	-	-	-	25.0	**33.3**	-	-	-
Cordia hirta	5	**0.3**	-	-	<0.1	40.0	**16.7**	-	-	100
Theobroma subincanum	2	**<0.1**	-	-	-	-	-	-	-	-
Leoncia glycicarpa	3	**0.1**	-	-	-	100	**100**	-	-	-
Couratea stellata	7	**0.1**	<0.1	<0.1	-	85.7	**83.3**	100	100	-
High Clay (HC)										
Jacaranda copaia	536	6.5	**31.8**	1.1	10.5	11.4	0.6	**4.5**	38.5	18.9
Solanum schlechtendalianum	79	0.2	**0.4**	<0.1	<0.1	46.8	23.2	**36.4**	83.3	100
Vernonia sp.	52	<0.1	**1.5**	-	<0.1	61.5	100	**74.5**	<0.1	100
High Phosphorus (HP)										
Croton palanostigma	244	-	0.7	**10.9**	0.2	21.3	-	-	**21.0**	28.6
Cassia spruceana	194	0.4	1.4	**7.1**	0.6	79.9	-	25.0	**80.5**	87.5
Tapirira guianensis	17	0.1	-	**1.4**	0.1	64.7	-	-	**87.0**	-
Maprounea guianensis	71	0.1	0.2	**0.8**	0.1	66.2	16.7	28.6	**70.2**	35.0
Alchornea triplinervea	31	0.2	-	**2.0**	0.5	25.8	-	-	**28.4**	25.0
Swartzia ingifolia	18	<0.1	0.1	**0.8**	-	66.7	-	100	**76.2**	-
Perebea mollis	13	<0.1	-	**0.2**	-	61.5	100	-	**55.3**	-
Ocotea leucoxylon	26	-	-	**3.2**	-	30.8	-	-	**24.1**	-
Low Phosphorus (LP)										
Vismia cayennensis	986	3.2	8.3	4.9	**23.4**	62.8	13.2	18.4	51.2	**62.2**
Guateria discolor	55	<0.1	0.1	<0.1	**0.6**	70.9	-	58.3	100	**73.5**
Bellucia spp.	170	1.5	1.2	0.1	**3.9**	18.8	6.3	5.2	-	**15.2**
Bocageopsis mutijuga	169	0.5	0.3	0.7	**2.7**	69.2	37.3	95.2	96.4	**97.8**
Astrocaryum aculeatum	7	-	-	0.6	**4.3**	0.0	-	-	-	-

DISCUSSION

Species composition in tropical successional forests can be highly variable. To what extent this variation is determined by environmental conditions remains to be clarified. In this study, we show that land-use intensity strongly determines species composition through a hierarchy of filters acting at early stages of succession and selecting for strong-sprouter species. Filtering effects of management practices and soil properties resulted in reduced species richness and beta diversity, implying that divergent successional communities are determined at early stages of succession. Consequently, the predictability of secondary succession will increase with land-use intensity.

Determinants of early species composition

Our analysis shows 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 major determinant, followed by clay content and phosphorus availability. An earlier study provided evidence that soils become less clayey and more nutrient-poor with repeated swidden-fallow cycles (Jakovac et al. 2015). In the present study, SF grouped by high clay content (HC group) being subjected to lower intensity of use (2 - 3 swidden-fallow cycles), and SF from the HP and LP groups being subjected to ≥3 cycles (Table 4.1). Hence, the species composition patterns reported here must be interpreted as resulting from interconnections of increasing number of cycles and decreasing soil quality (Table 4.1).

This study evidences the significance of soil quality to determine species composition of secondary forests. The relation between soil properties and species composition has been seldom evaluated in secondary forests, with studies reporting contrasting results (Buschbacher et al. 1988, Feldpausch et al. 2004, Lawrence 2005b, Gomes and Luizão 2012). This 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, Feldpausch et al. 2007). Our sampling design, in which we excluded the effect of successional age, allowed for a better balance among the other factors, and therefore, a higher detectability of the relative effect of soils on plant community.

Species-environment relationships and the role of sprouting ability

In agreement with our hypothesis, this study shows that increased management intensity not only select for resprouters at the individual level (Jakovac et al. 2015) but also filters out seed-dependent species and favours strong-sprouter species (Figure 4.2, Table 4.2). Although most tropical forest species are able to resprout (Kauffman 1991, Poorter et al. 2010), only a few can resprout after losing its aboveground biomass repeatedly (Hooper et al. 2004); such species are called strong sprouters (Bond and Midgley 2001). Strong sprouters hold a strategy that allows persistence in fire-prone ecosystems (Bond and Midgley 2001), and under repeated cutting and burning cycles (this study). Accordingly, strong-sprouter species characterized assemblages regenerating after higher management intensity (HP and LP groups) (Table 4.2).

Species assigned as indicators of each plant assemblage had different sprouting ability but also differed in other traits, such as maximum height and the capacity to cope with low soil quality (Figure 4.1). Therefore, evaluating these species-environment relationships can help explain the mechanisms underlying shifts in species composition (De'ath 2002). Most indicator species were widely distributed across the sampled landscapes (Table 4.2) but were favoured under specific environmental conditions. These conditions were unrelated to landscape configuration (Figure 4.1), agreeing with other studies showing that distance to the old-growth forest does not affect the distribution of early pioneers (Guariguata et al. 1997, Holl et al. 2000, Benítez-Malvido et al. 2001). Interestingly, these species favoured by land-use are a subset of the regional species pool (Table 4.2), rather than exogenous species that could invade and dominate degraded lands (Schneider and Fernando 2010).

Cecropia sciadophylla and *Jacaranda copaia* characterized SF associated with low use intensities ($\leq$ 3 cycles) and higher soil quality (Table 4.1). Sites that had experienced only one cycle were dominated by *C. sciadophylla*, which is a fast-growing pioneer that grew up to 16 m height in 5 years, mono-dominating the canopy of these SFs. After 2-3 cycles, on clayey soils, *J. copaia* was the indicator and most dominant species (30% of basal area) (Figure 4.1). *J. copaia* is also a fast-growing pioneer (achieving ca. 17 m in 5 years) but differs from *C. sciadophylla* in that it shared the canopy layer with other species. As poor resprouters, which had less than 10% of resprouting individuals (Table 4.2), these two species are eliminated by repeated cutting and burning practices. *C. sciadophylla* is especially susceptible to such practices, exclusively dominating one-time-burned areas as shown in this study and in other areas of the Amazon region (Steininger 2000, Mesquita et al. 2001, Peña-Claros 2003, Hooper et al. 2004). Additionally, as fast growers, in height and diameter (Popma and Bongers 1988), these species probably require relatively high nutrients availability (Gomes and Luizão 2012) and may not be competitive under lower soil quality.

While some species were excluded by land-use intensification, others were favoured. *Croton palanostigma* and *Cassia spruceana* characterized SF at sites subjected to higher land-use intensity (Figure 4.1) and lower soil quality than the previous groups Cy and HC (Table 4.1), but with relatively higher phosphorus availability than the LP group. These two species were found either sharing the canopy of these secondary forests or mono-dominating it, achieving around 9 m height in 5 years of succession. These species are being favoured by land use, due to their capacity to resprout (Table 4.2), but may not be able to cope with extremely low phosphorus availability like *Guateria 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 phosphorus availability (Condit et al. 2013), in the distribution of tropical rainforest species (John et al. 2007, Dalling et al. 2012, Toledo et al. 2012). *Vismia cayennensis* was the dominant species of the SF over low phosphorus availability. It made 23% of the total basal area, and formed the canopy of these SF, which had on average 9 m height. *Vismia cayennensis* has a well-developed root system with long and tick roots (Pavlis and Jeník 2000) that allows stump and clonal resprouting. This developed root system along with associations with mycorrhiza may enhance phosphorus uptake in *Vismia* spp (Freitas 2005). High dominance of *Vismia* species has been associated with abandoned pasturelands (Mesquita et al. 2001, Barlow et al. 2007), but here we show that intensive shifting cultivation can also engender *Vismia*-successional pathways under poor soil quality.

Given that plants show a trade-off between investing in growth or in storage roots, species able to repeatedly resprout are usually slower growing (Bond and 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 outcompeted 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 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) to survival (to disturbance).

Mechanisms underlying divergent pathways

Alternative successional pathways in the Amazon have been reported to continue to diverge during the first three decades of succession (Longworth et al. 2014, Williamson et al. 2014). Plant communities regenerating on clear-cuts rapidly diversified, 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 divergent characteristics related to species composition, species diversity and regeneration strategies, indicating that the foundations of divergent pathways are at the onset.

Initial floristic composition is known to play an important role in determining further species turnover in successional forests (Peña-Claros 2003). At 5 years of succession under *C. sciadophylla* and *J. copaia* canopies we observed a rather high alpha and beta-diversity (Figure 4.2), which certainly arouse from the assorted legacies left from the old-growth forest. These legacies will continue to play a role in further species diversification (Peterson and Carson 2008). With increasing land-use intensity, however, we showed that this diversity is reduced to a narrower set of species (Figure 4.2). When a diverse community is lacking at the onset and regeneration depends mainly on resprouters, diversification 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 and Aide 2001, Wieland et al. 2011) and the position of intensively used sites in fragmented and deforested landscapes (Robiglio and Sinclair 2011), species build-up is bound to be slow in these areas. Although environmental conditions and biotic interactions may also affect species recruitment (Kabakoff and Chazdon 1996, Slocum 2001, Walker et al. 2010a, Lebrija-Trejos et al. 2011) and contribute to sustain divergence through time, the great impact of land use at the onset will hardly be mitigated by natural regeneration itself. This study supports the idea that filtering processes acting early in succession are primarily responsible for driving and sustaining alternative successional pathways.

Land-use history to increase predictability

The lack of a good record on past land-use may be one of the reasons for chronosequence studies to 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 divergence 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 past land use and could therefore be used as indicators of land-use intensity in rapid field assessment or to validate land-use history. The fact that SF sampled in five different villages were grouped by land-use intensity indicates that land use was stronger than geographical location in determining early species composition. Our early plant communities are largely composed by pioneer species with wide-spread 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 geographical scales within the Amazon region. 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 indicator of increasing levels of land-use intensity in the Central Amazon region and beyond.

CONCLUSION

Species composition of secondary forests is strongly determined by land-use intensity. Hierarchical effects of management intensity and associated reduction in soil quality filters out seed-dependent species and favours strong sprouters and species that can cope with low nutrient availability. This filtering effect reduces diversity at the local and regional scale. As a consequence, with increasing land-use intensity, secondary forests become more similar to each other and secondary succession becomes more predictable. This study enlightens mechanisms through which different land-use intensities lead to alternative successional pathways in the Amazon.

ACKNOWLEDGEMENTS

We thank Paulo Apóstolo Assunção for assistance with species identification. The authors are indebted to the inhabitants of the villages Vila Sião, São Francisco, São Sebastião, Nogueira and Agrovila who authorized and contributed to this research. We are also grateful to Reney, Mrs. Rosa and Mr. Falcão for assisting during field work and to Mr. Falcão, Mr. Ilson and Mr. Armelindo families for kindly hosting the field expeditions. We also thank the Instituto Chico Mendes de Conservação da Biodiversidade for authorizing this research to be held at the National Forest Reserve FLONA Tefé and for logistic support during field expeditions. This research was funded by The Netherlands Fellowship Program (NFP-NUFFIC).

The first author (C.C.J.) received scholarships from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (Br) through the Instituto Nacional de Serviços Ambientais da Amazônia – SERVAMB and from Wageningen University (NL).


Miss Butterfly

Chapter 5

Swiddens under transition: consequences of agricultural intensification in the Amazon

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Submitted for publication

ABSTRACT

Swidden cultivation is the traditional agricultural practice in the tropics. Due to socio-economic changes, swiddens are either abandoned, substituted for other agricultural systems, or intensified. We evaluated how agricultural intensification affects traditional swidden cultivation in the middle Amazonas River region, one of the main cassava producing areas in the Brazilian Amazon. We hypothesized that agricultural intensification leads to changes in management practices, to an increase in weed cover and weeding labour demand, and to a reduction in cassava yield. Based on participant observation and semi-structured questionnaires applied to 28 farmers we characterized the current management practices. Based on surveys of 28 swiddens previously subjected to different numbers of swidden-fallow cycles, we evaluated the effects of intensification on swidden size, cassava production, weed pressure and weeding effort. We also evaluated in these swiddens the chemical and physical soil properties and the cassava nutrient content. Our results show that with increasing number of swidden-fallow cycles, cassava yield decreases, weed cover increases and weed composition changes, with decreasing cover by trees and increasing cover by hard-to-weed graminoids. Changes in weed composition and weed regeneration strategies result in increased weeding labour demand. Although swidden cultivation systems can be highly adaptable, in our study area the ongoing agricultural intensification is leading to lower swidden productivity without ensuing clear benefits for farmers. Maintaining swidden cultivation while assuring reasonable labour productivity requires management practices to be adapted. Diversifying production and income and improving fallow management could increase the resilience of the system.

KEYWORDS: Shifting cultivation, weeds, cassava, labour, yield, Brazil.

INTRODUCTION

Swidden cultivation is the traditional agricultural system in the tropics. Since the 1970's, this system is undergoing transformations due to population growth and changes in market demand (Mertz et al. 2009, Padoch 2010). In response to those drivers, swiddens are either abandoned, replaced by other agricultural systems, or intensified (van Vliet et al. 2012). Agricultural intensification of swidden cultivation is mainly achieved by increasing the frequency of swidden-fallow cycles and shortening the fallow periods (Coomes et al. 2000, Schmidt-Vogt et al. 2009).

Changes in the balance between cropping and fallowing periods due to intensification can threaten the sustainability of swidden cultivation. In traditional systems where no external inputs are applied, swidden potential productivity is basically dependent on intrinsic soil fertility, plus the nutrients released from the burned fallow biomass. Actual agricultural productivity is then further reduced by weeds, pests and pathogens. Secondary-forest regrowth during fallow periods is able to partially recover nutrients that had been leached to deep soil layers, and that had been adsorbed to clay particles during the cropping period, and to suppress the weed seed-bank under its closed canopy (de Rouw 1995). Repeated swidden-fallow cycles and shortened fallow periods can result in a gradual decrease in soil fertility (Arnason 1982, Runyan et al. 2012) due to nutrient losses by burning, cropping and leaching (Nye and Greenland 1964, Jordan et al. 1983, Holscher et al. 1997), and thereby to reduced fallow regrowth rate (Lawrence 2005a, Jakovac et al. 2015). Consequently, nutrient availability may be reduced (Silva-Forsberg and Fearnside 1997, Bruun et al. 2006, Styger et al. 2007) and weed infestation increased (de Rouw 1995, Dingkuhn et al. 1999).

Increased weed infestation is one of the main causes of poor crop development and increased labour demand, and both of these are strong reasons for farmers to leave swiddens to fallow (Staver 1991, de Rouw 1995, Ekeleme et al. 2004). Weed infestation is, therefore, an essential component of labour productivity in systems where weed control is based on manual weeding through family labour (Netting 1993, Vissoh et al. 2007). But the implications of weed infestation depend on a complex interplay between the weed community and farmer perception (Vissoh et al. 2007). Weeds can be defined as spontaneous plants growing on cropping fields where and when farmers do not want them, and may comprise every plant that is not a crop (Vissoh et al. 2007). In traditional swidden systems in the Amazon, many spontaneous plants are perceived as useful and are managed within swiddens instead of being weeded (Denevan and Padoch 1987). Therefore, how agricultural intensification will affect the traditional swidden cultivation system will be a product of how the weed community and farmer perception of weeds will change with intensification.

Agricultural intensification in the Amazon has not been well documented (Vosti et al. 2002, van Vliet et al. 2013), implying that its consequences for the local traditional systems are poorly known (Emperaire and Eloy 2015). Most studies on this subject have been conducted in Asia and Africa, where population growth has been pushing traditional agriculture towards intensification since decades. In this context, we evaluated here how agricultural intensification affects management practices and swidden productivity in traditional systems in the Central Amazon. We hypothesised that agricultural intensification will lead to important changes in the way the system is managed, to a decrease in swidden productivity and crop yield, and an increase in weeding-labour demand. We used measurements of weed cover and weeding frequency as proxies for weeding effort. Because weeding demand not only depends on the biomass of weeds but also on their identity and on how they are managed, we evaluated the weed community and interviewed farmers about their weeding practices and perception of the weed community. By integrating quantitative and qualitative data on swiddens along a gradient of agricultural intensification, we aimed to improve the understanding on the effects of agricultural intensification on swidden cultivation systems.

METHODS

Study area

We carried out this study along the Tefé river and its tributaries. The Tefé river is a tributary of the Amazonas river located at its middle region, in the Central Amazon, Brazil. The region of the middle Amazonas River is one of the largest producers of cassava flour in the Brazilian Amazon. Cassava flour, known as *farinha,* is the main source of carbohydrates in rural and urban areas of the Brazilian Amazon (Dias et al. 1998). *Farinha* is produced from processed bitter cassava (*Manihot esculenta* Crantz), which is cultivated and processed by smallholder farmers (Dias et al. 1998). We conducted the study in 5 riverine villages: Vila Sião, São Francisco, Jauarituba, Monte Carmelo and Agrovila, which are located between 15 and 50 km from the largest city Tefé. Villages are inhabited by *caboclos* (Adams et al. 2009) who cultivate swiddens in non-flooded areas (*terra firme*) on oxisols and ultisols.

Data collection and analyses

We performed participant observation during three field expeditions of 15 - 30 days each and carried out semi-structured interviews with 28 farmers owning the surveyed swiddens. Field work took place during 2011 and 2013, with swidden survey being done in June and July 2013. The semi-structured questionnaires had open questions on swidden land-use history, cultivation, labour and management practices, and more detailed questions on weeding practices. Interviews were done on the swidden location so farmers could point out the crops, cassava landraces and weed species mentioned and could better recall the dates, labour and management practices applied to that specific field. We combined information from participant observation and interviews to describe the system and its labour and management practices. We calculated weeding effort as the number of weedings done within one cropping period.

To evaluate the effects of agricultural intensification on swidden productivity, we sampled 28 swiddens along a gradient of agricultural intensification, represented by varying numbers of previous swidden-fallow cycles (1 to 10 cycles). At each swidden, we determined cassava yield, cassava leaf nutrients, and soil chemical and physical properties. In 22 of these swiddens we also evaluated crop and weed cover. We recorded the geographical position and the borders of each swidden using a GPS (Garmin eTrex Vista HCx), which was later used to calculate swidden area using ArcGIS 10.1 (ESRI 2012).

We estimated crop and weed cover using the point intercept method (Goodall 1952). At the centre of each swidden we located two 50 m long transects at least 15 m apart. We walked each transect placing a graded vertical pole of 2.5 m height at every 1 m (sampling point), so each transect had 50 sampling points. At each sampling point, we recorded all heights at which plants touched the pole, and identified each plant to the lowest taxonomic level possible. Later, we classified the species into crops or weeds. We considered as weeds every spontaneous plant that was not considered by farmers as a crop. Spontaneous plants (weeds) considered useful by farmers were identified during interviews. Within weeds we recognised four life forms: forbs, graminoids (Cyperaceae, Commelinaceae and Poaceae), woody plants (including trees, shrubs and palms), and climbers (vines and lianas). We then calculated crop and weed cover as the summed number of contacts of each plant type to the pole along the transects; contacts at different heights were also summed up. We took the average of the two transects sampled at each swidden. We represented crop cover as the absolute cover, and weed cover by its percentage relative to total plant cover (crops plus weeds). We calculated the percent cover of the four weed life-forms relative to total weed cover. Additionally, we calculated the percentage of sampling points where cassava was the highest plant touching the pole, as a proxy for competition for light.

To calculate cassava yield, we randomly placed 10 sampling plots of 9 m^2 at each swidden. At each sampling plot, we counted the number of cassava individuals and identified its landrace. Then, we selected two cassava individuals from the dominant landrace, *Catombo*, to take detailed measures. From these two individuals, we measured height, basal area and fresh-root weight (n = 20 individuals per swidden). Fresh roots were weighed using a digital hanging scale with 0.10 Kg precision. We calculated cassava fresh-root weight as the average weight per plant within each swidden. Swidden yield was calculated as the mean fresh-root weight multiplied by the average planting density per swidden.

From one of the two harvested cassava plants, we sampled two leaves for plant nutrient analysis (n = 10 samples per swidden). We selected fully expanded leaves located at the top of the crown, receiving full sunlight and with no signs of herbivory. We stored the cassava leaves in paper bags and dried them in a field oven for ca. 48 hs. At each swidden we also collected one composite soil sample, composed of 5 sub-samples from the first 20 cm soil depth. Soil samples were air-dried and stored in plastic bags. Plant nutrient and soil properties were analysed by EMBRAPA soil laboratory in Manaus, according to published protocol (EMBRAPA 2011). Plant nutrients assessed were N, P, K, Ca and Mg. Soil nutrients and texture parameters assessed were: soil organic carbon, total N, available P, K, Ca, Mg, Fe, Al and pH, and the percentages of sand, silt and clay.

Statistical analyses

We summarised the soil data using Principal Components Analysis (PCA), where the above-assessed variables were included. We then used the scores of the first and second axes of the PCA to represent soil properties for further analyses. The first two axes of the soil PCA explained 55.5% of variation. The first axis explained 31.8% and represented a texture gradient, hereafter referred to as *soil texture axis*; the second axis explained 23.7% and represented a gradient in pH and cations. The second axis will be referred to as *soil pH axis*.

To evaluate the effect of agricultural intensification on crop and weed cover, weeding effort, swidden size and agricultural output, we applied a series of multiple linear regression analyses. We included as independent variables the number of swidden-fallow cycles, previous fallow-period length and the scores of the soil texture and pH axes. Previous to analysis we had checked for multicollinearity. We then tested the effect of these variables and their interactions on: cover of crop, weeds and the different weed life-forms (forbs, graminoids, climbers, and woody plants), as well as on weeding effort, cassava fresh-root weight and swidden yield. We used a stepwise (both backward and forward) procedure to select the best and most parsimonious model for each response variable, based on Akaike information criteria (AIC) and by keeping only the significant predictors in the final model. Multiple regression analyses were done using the *step* function in R package *leaps* (R-Development Core Team, 2010). PCA was done in CANOCO 5.0 (Ter Braak and Smilauer 2012). Percentage data were transformed by the arcsine of the square root prior to analyses.

Yearly cassava flour (*farinha*) production per household was estimated by multiplying the mean cassava yield (kg) and mean swidden area (ha) measured in the field, considering that households usually cultivate one field per year (section 3.3). *Farinha* production was calculated based on an estimated production of 0.35 kg of *farinha* per kilo of cassava fresh-root (Dias et al. 1998, Embrapa 2006). Additionally, we estimated household income along the gradient of intensification. Household income was estimated based on estimated *farinha* production and on the average *farinha* price paid to farmers during the study period, at the study site (2011-2013). Prices were converted from Brazilian real (BRL) to US dollars (USD) based on the average exchange rate for the study period (BRL/USD = 0.52; OANDA Rates^{TM}).

RESULTS

Swidden cultivation in the middle Amazonas river

The main activity in these villages is bitter-cassava cultivation for the production of *farinha*. *Farinha* is destined for both consumption and trading for 96% of these farmers. The villages are connected to the market economy through the presence of middlemen.

In every community, bitter cassava was the dominant crop. We found nine landraces of bitter cassava in 28 swiddens, named: *Catombo, João Gonçalo, Aparecida, Baixotinha, Sete homens, Pagoinha, Sacaí, Jabuti*, plus an unnamed one. Per swidden, the number of landraces varied from one to four, with a dominance by *Catombo*. This landrace was found in every swidden and was always the dominant one. Farmers' preference for *Catombo* was related to the marketability of the *farinha* as well as its good productivity on poor soils and its flexible harvesting period (from 9 to 24 months post-planting, although in most cases harvesting is after around one year). A few other crops were occasionally planted along with cassava, always in low densities, and exclusively meant for self-consumption: sweet cassava (*Manihot* *esculenta*), pineapple (*Ananas* spp.), banana (*Musa* spp.) and four varieties of yam (*Dioscorea* spp.).

Farmers reported that they manage swidden cultivation with short fallow periods of around 5 years (ranging from 3 to 8 years, but very occasionally fallow periods can be longer or even shorter), and short cropping periods of 1 to 3 years. They also reported that longer fallow periods (> 8 yrs) would be preferred but due to shortage of land they are shortening it. Each household opens one to two swiddens per year that vary between 0.5 and 2 hectares. Farmers reported that swidden size depends on factors such as his/her economic conditions because of the costs involved in establishing and maintaining the field, and on weed pressure with smaller fields being opened in more weed-infested areas.

Cassava is cultivated without external inputs, such as fertilizers or herbicides. Labour is still mostly based on family and collective work (locally named *ajuri* or *mutirão*) but is currently changing (see next section). When asked what was the most laborious activity in cassava swidden-fallow cultivation, harvesting and processing, most farmers mentioned weeding (67%), followed by processing cassava into *farinha* (18%). There was consensus why weeding was the most laborious activity: working long hours in an unpleasant crouched position under harsh conditions of full sunlight is tiring and back-hurting.

Weeding practices

The laboriousness of weeding was related to the type of labour applied. Planting labour was mostly based on collective (51%) and family (30%) work, but weeding was mainly done by the close family (63% of the farmers) or paid workers (37%), but not by collective work. Farmers stated that weeding collectively is becoming less common due to its laboriousness. Depending on the type of labour applied, estimations of time spent on weeding one hectare varied from one week (1 person working full days) up to three months (one or few people working few hours per day). Usually, when done by the farmer with his/her family, swiddens are not weeded all at once but sparsely in time, by working a few hours per day during several weeks. Farmers reported that if weed infestation is too high and rapid, they may not be able to control it in large swiddens. Therefore, weed infestation is a constraint to swidden size.

Weeding is done by pulling out and machete-cutting weeds (96%), and less commonly also by using a hoe (29%). All farmers stated to pull out most of the weeds, in order to delay next infestation, and machete-cut only those that cannot be easily pulled out either because they are strongly rooted or too spiny. When asked about the most problematic weeds, graminoids (Cyperaceae and Poaceae) were most cited (75%), followed by a liana (*Cissus erosa* - Vitaceae) (35%) and an erect Asteraceae forb (35%). Reasons for citing these weeds were mainly related to fast and wide-spread infestation and to the difficulty of controlling infestation because of vigorous resprouting from any part of the rhizome that is occasionally left behind. Additional reasons were that graminoids and the Asteraceae forb can easily take over the swidden if infestation is not early controlled, and the liana can hamper cassava development and is difficult to detach without damaging the cassava branches.

Selective weeding was a major practice among farmers (62%), while 38% stated to clean-weed. Only three species of spontaneous plants were maintained in the swiddens because of the provision of goods: Tucumã (*Astrocaryum aculeatum*, Arecaceae; highly appreciated fruits for self-consumption), Brazil nut (*Bertholletia excelsa*, Lecythidaceae; nuts for self-consumption and commercial) and Envira (mainly *Guatteria* spp., Annonaceae; bark used for manufacturing the strap of baskets (*paneiros*) used to carry the harvested cassava from the field to the processing place (*casa de farinha*)).

Effects of agricultural intensification on swiddens

Swiddens were strongly affected by agricultural intensification. Number of swidden-fallow cycles was the only significant factor affecting swidden size, crop and weed cover, cassava size and yield, and weeding effort, in multiple regression analyses (Table 5.1). Soil texture, soil acidity (Appendix Figure A5.1) and previous fallow period were not significantly related to any tested variable.

Swiddens had an average size of 0.92 hectares (0.68 SD; Table 5.2), and this decreased significantly with number of cycles (Table 5.1; Figure 5.1d). Swiddens larger than one hectare were only found up to the 3rd swidden-fallow cycle (Figure 5.1d). Reduction in swidden size was attributed by farmers to increased weed infestation (see previous section), similarly to what was detected in our regression analyses. With increasing number of swidden-fallow cycles crop cover decreased and weed cover increased (Table 5.1; Figure 5.2). Moreover, weed community composition changed, with graminoids cover increasing and woody plants (mainly trees) cover decreasing with number of cycles (Table 5.1; Figure 5.2). The number of weedings varied from 1 to 3 within one cropping period, and increased with number of swidden-fallow cycles (Table 5.1).

The decrease in crop cover was related to decreased cassava performance with agricultural intensification. After one or two cycles, cassava was the highest plant in the vegetation profile, dominating the canopy (Figure 5.1c). But with increasing number of cycles cassava canopy dominance significantly decreased (Table 5.1; Figure 5.1c). This change in cassava canopy position was related to poorer performance of cassava with increasing intensification. Cassava height, basal area and fresh-root weight were positively correlated with each other (Appendix- Table A5.1) and altogether decreased with number of previous cycles (Table 5.1).

Table 5.1. Effects of number of swidden-fallow cycles on swiddens in Central Amazon, Brazil. Results from linear regression analyses of crop and weed cover, swidden size, weeding effort, cassava fresh-root weight and yield as a function of number of swidden-fallow cycles (which was the only predictor retained in the multiple regression analyses). For each significant regression model, the degrees of freedom (d.f.), overall model estimates (r squared, adjusted r squared and P-value) and estimates of slope, standard error (SE), t and P-values of the intercept and the significant predictor (number of cycles) are provided.

Response variable	d.f.	R^2	P-value	Intercept		Number of cycles		
				t	P	Slope (SE)	t	P
Crop cover (absolute)	20	0.29	0.010	10.24	<0.001	-6.70 (2.35)	-2.85	0.010
Crop cover (%)	20	0.18	0.050	11.42	<0.001	-0.04 (0.02)	-2.09	0.050
Weed cover (%)	20	0.18	0.050	6.60	<0.001	0.04 (0.02)	2.08	0.050
Woody cover (%)	20	0.20	0.038	11.12	<0.001	-0.03 (0.01)	-2.21	0.039
Graminoid cover (%)	20	0.26	0.016	4.07	<0.001	0.04 (0.18)	2.63	0.016
Forb cover (%)	20		ns					
Liana cover (%)	20		ns	13.95	<0.001			
Crop dominance	20	0.25	0.018	13.70	<0.001	-0.03 (0.01)	-2.58	0.020
Swidden size	26	0.20	0.018	6.13	<0.001	-0.13 (0.05)	-2.51	0.019
Weeding per month	26	0.146	0.048	7.27	<0.001	0.01 (0.004)	2.07	0.048
Cassava fresh-roots weight	26	0.26	0.005	18.63	<0.001	-0.07 (0.02)	-3.06	0.005
Cassava yield	26	0.25	0.006	16.79	<0.001	-0.72 (0.24)	-2.95	0.006

Individual cassava fresh-root weight varied from 0.15 to 5 kg per plant, with averages per swidden varying from 0.90 to 2.25 kg (Table 5.2). Although swiddens varied in time post-planting (8 - 11 months), time post-planting was unrelated to cassava fresh-root weight (Table A5.1). Average cassava fresh-root weight decreased significantly with number of cycles (Table 5.1), which resulted in a significant reduction in swidden yield (Table 5.1, Figure 5.1b). Cassava yield decreased from 23.8 ton ha^{-1} to 9.4 ton ha^{-1} with number of cycles, but had a peak at two cycles (Figure 5.1b). This increase in yield from one to two cycles was acknowledged by farmers, who associated it with a higher fire intensity at the second cycle when laying forest-logs are drier and the fine root layer covering the forest soil is eliminated. Yield was unrelated to nutrients in the leaves and to both soil PCA axes, but was related to cation content (Table A5.1). Nutrient contents in cassava leaves varied less than soil contents (Table 5.2), and were not correlated (Table A5.2). Planting density did not change with number of cycles nor with swidden size (Table A5.2).

Estimated household income also decreased with number of cycles (Figure 5.3). Based on interviews, we considered each household to cultivate one field per year. *Farinha* prices paid to farmers varied from 0.78 US$ kg^{-1} (1.50 R$ kg^{-1}) to 2.08 US$ kg^{-1} (4.00 R$ kg^{-1}) during 2011 - 2013, with an average of 1.43 US$ kg^{-1} (2.75 R$ kg^{-1}). As a consequence of decreased cassava yield and swidden size with number of cycles (Figure 5.1), estimated household income also decreased (Figure 5.3). Estimations of average household income, based on average *farinha* prices during the study period decreased from ca. 14,000 US$ at 2-cycles to around 4,000 US$ after 5 cycles (Figure 5.3).

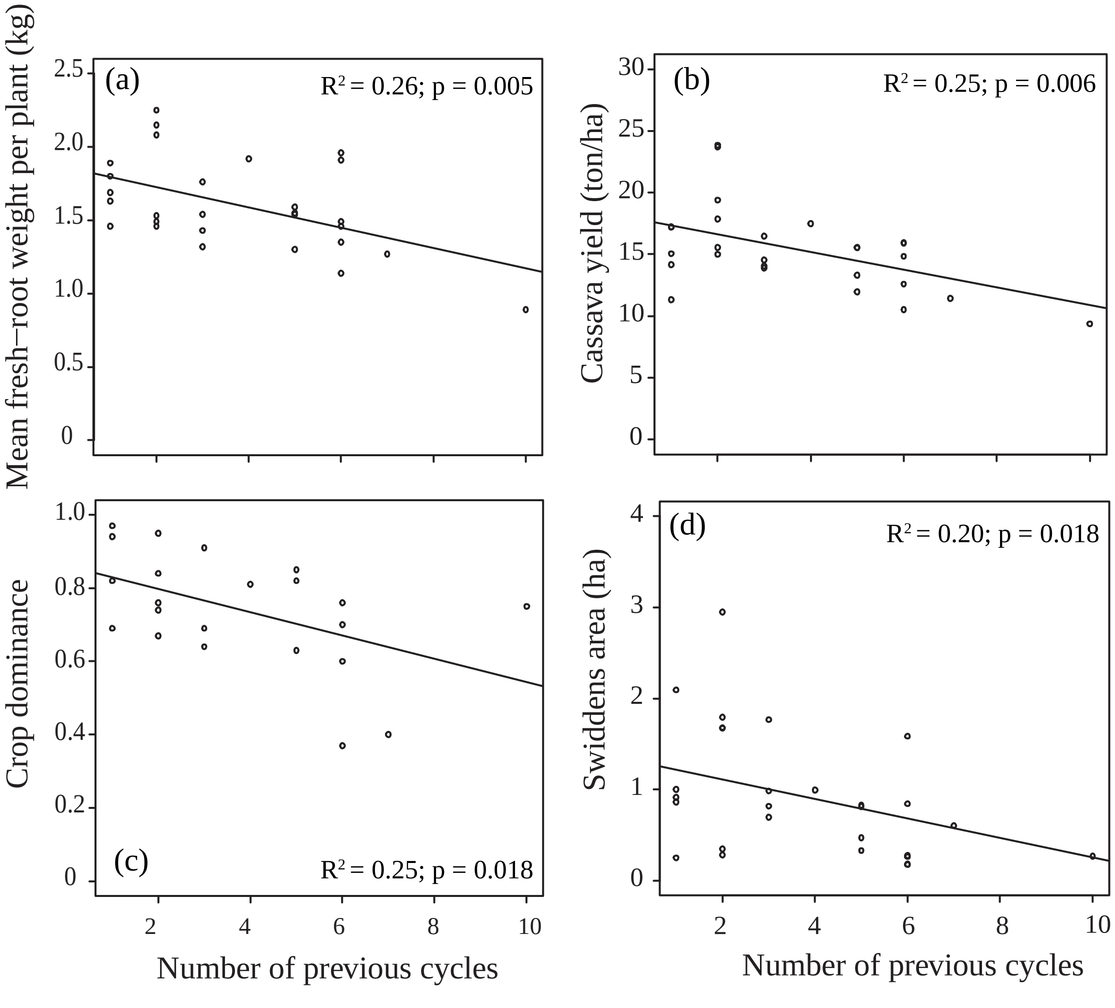


Figure 5.1. Cassava yield, canopy dominance and swidden size as a function of number of swidden-fallow cycles in Central Amazon, Brazil. Changes in cassava mean fresh-root weight (a), cassava yield (b), cassava canopy dominance (c) and swidden size (d) with number of swidden-fallow cycles.

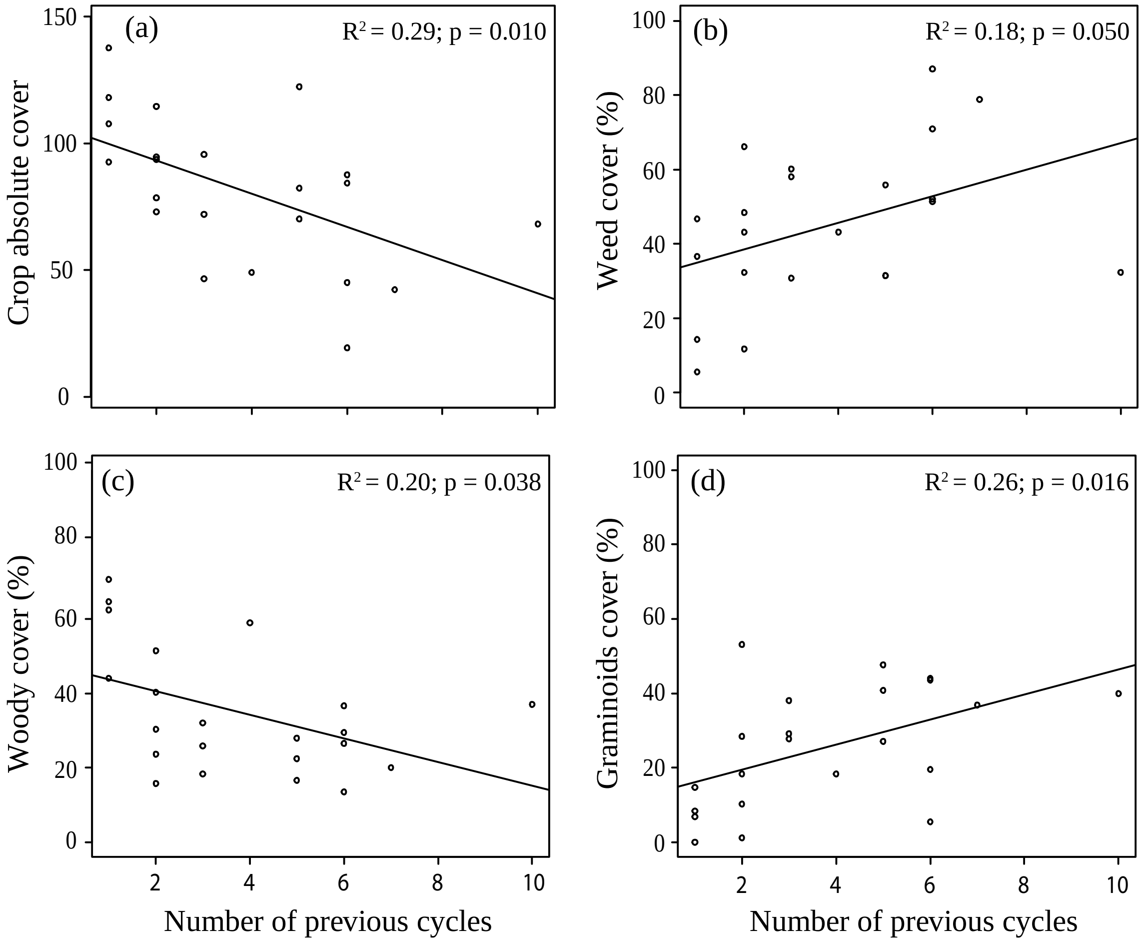


Figure 5.2. Changes in crop and weed cover with number of previous swidden-fallow cycles. Absolute crop cover expressed in number of intercepted points along the cover transects (a); Percentage of weeds cover relative to total swidden cover (b); percentages of woody (c) and graminoid (d) weeds relative to total weed cover, as a function of number of previous swidden-fallow cycles. Swiddens were surveyed in 2013 in the Central Amazon, Brazil.

Table 5.2. Characteristics of swiddens and cassava production in Central Amazon, Brazil. Means, standard deviation (SD), minimum (Min) and maximum (Max) values and coefficient of variation (CV) are presented for the following group of parameters: management, soil properties, cassava leaf nutrient content, and cassava development. Data were collected at 28 swiddens surveyed in 2013.

Variable	Mean (SD)	Min	Max	CV
Management practices				
Number of cycles	3.8 (2.3)	1.00	10.00	0.60
Previous fallow age (yrs)	5.6 (3.5)	1.00	20.00	0.61
Time post-planting (days)	274.0 (26.4)	226.0	335.0	0.10
Swiddens size (ha)	0.92 (0.7)	0.18	2.95	0.74
Soil properties				
Sand (%)	52.0 (12.2)	27.7	77.5	0.24
Clay (%)	18.3 (6.01)	8.60	31.4	0.33
Silt (%)	29.6 (9.2)	13.9	50.2	0.31
C (g kg^{-1})	15.25 (3.2)	8.24	21.3	0.21
N (g kg^{-1})	1.26 (0.3)	0.67	1.74	0.22
P (mg dm^{-3})	2.39 (0.9)	1.00	5.00	0.36
K ($cmol_c$ dm^{-3})	0.11 (0.04)	0.04	0.28	0.37
Ca ($cmol_c$ dm^{-3})	0.12 (0.1)	0.05	0.57	0.83
Mg ($cmol_c$ dm^{-3})	0.22 (0.1)	0.09	0.58	0.53
Al ($cmol_c$ dm^{-3})	3.99 (1.1)	1.88	7.39	0.28
Sum of bases ($cmol_c$ dm^{-3})	0.45 (0.2)	0.21	1.29	0.49
CEC ($cmol_c$ dm^{-3})	4.45 (1.1)	2.24	7.69	0.24
Al saturation (%)	89.2 (5.61)	67.7	96.1	0.06
pH	4.19 (0.2)	3.82	4.77	0.06
Leaf nutrients				
N (%)	3.98 (0.18)	3.68	4.27	0.05
P (%)	0.28 (0.03)	0.18	0.31	0.11
K (%)	1.34 (0.14)	1.03	1.56	0.10
Ca (%)	0.41 (0.08)	0.25	0.57	0.19
Mg (%)	0.28 (0.03)	0.22	0.35	0.10
N:P ratio	14.65 (1.9)	13.0	22.9	0.13
Cassava development				
Planting density (cassava ha^{-1})	9,658 (1,401)	7,222	13,333	0.15
Fresh-root weight (kg)	1.6 (0.3)	0.89	2.25	0.19
Cassava height (m)	2.36 (0.4)	1.55	3.11	0.16
Cassava basal area (cm^2)	4.97 (1.2)	2.79	7.30	0.23
Cassava yield (ton ha^{-1})	15.35 (3.3)	9.37	23.85	0.21

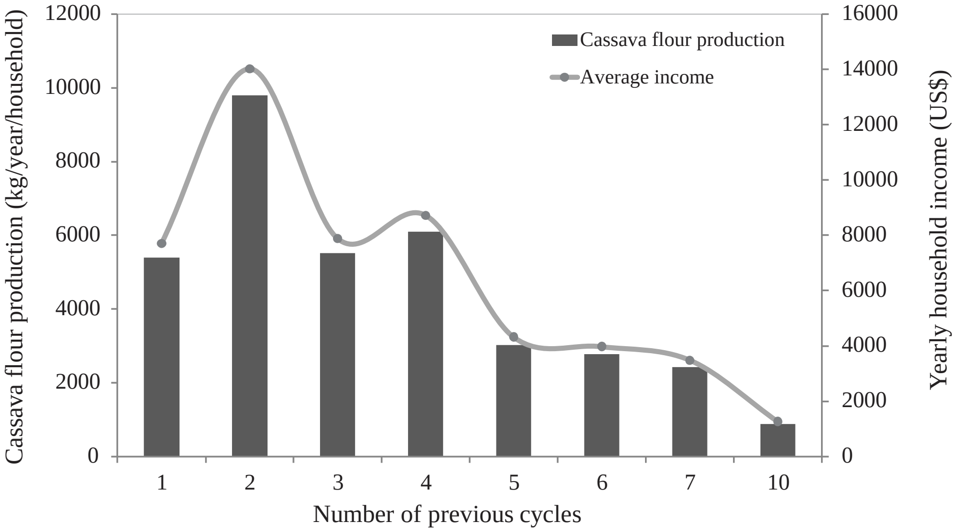


Figure 5.3. Estimated household cassava flour (farinha) production and income per year along a gradient of agricultural intensification. Cassava flour production (bars) was estimated for different number of cycles, based on mean cassava yield and swidden area, measured in the field (Figure 5.2b and d), considering that each household cultivates on average a single field per year. Income was estimated based on average cassava flour production and on average prices paid to farmers (average R$ 2.57; US$ 1.43) during 2011-2013, at the region of the middle Amazonas river, Central Amazon, Brazil. Prices were converted to US dollars based on average exchange rate for the period (BRL/US$ = 0.52).

DISCUSSION

A system under transition

Swidden agriculture in the middle Amazonas River region is under transition. The studied sites kept characteristics of traditional swidden cultivation, but had simplified management practices and low crop diversity. Characteristics of a traditional system such as the production of staple food, family and collective work, dependency on manual labour and rudimentary tools, and absence of external inputs or machinery still prevail in the area. But the swiddens we studied are much less diverse in crops and cassava landraces than traditionally managed ones (> 15 annual crops) reported for various areas of the Amazon (Denevan and Padoch 1987, Emperaire and Eloy 2015). Loss of crop diversity is a common consequence of market orientation (Pereira and Lescure 1994, Peroni and Hanazaki 2002, Rerkasem et al. 2009). In the studied area, farmer preference for one cassava landrace was related to marketability of the flour (*farinha*) and cultivation characteristics (Lima et al. 2012). Additionally, the focus on cassava as the main product reduces farmer interest in other species, such as other crops (Rerkasem et al. 2009) and beneficial 'weeds' that could complement household income (Pereira and Lescure 1994).

The need to produce for both consumption and trading coupled with a shortage of suitable land results in intensification, which can be noted from shortened fallow periods and increased frequency of swidden-fallow cycles. In many cases, market integration has led to the demise of swidden cultivation and its replacement by cash crop cultivation on more permanent land use (Padoch et al. 2007, Rerkasem et al. 2009, Ziegler et al. 2009, van Vliet et al. 2012). In our study area, intensification is associated with the transformation of the staple towards a cash crop. Increased market interest in the traditional crop could provide opportunities for conserving traditional agriculture (Hansen and Mertz 2006, Emperaire and Eloy 2015). Our study shows, however, that the ongoing intensification is currently encompassing important negative impacts to the sustainability of swidden cultivation and to farmer livelihoods.

Changes in weed community and weeding practices

With increasing number of swidden-fallow cycles, crops are overtaken by hard-to-eradicate weeds, despite increased weeding frequency (Table 5.1). Higher weed infestation was directly related to a change in life-form composition from tree-dominated towards graminoid-dominated communities (Figure 5.2), corroborating studies in other systems (de Rouw 1995, Trichard et al. 2013). Such changes in life-form composition are also related to changes in plant regeneration strategies, with sprouting and stoloniferous species being favoured under high land-use intensity (Jakovac et al. 2015). Therefore, changes in weed infestation, composition and regeneration strategies have consequences for weed management and labour practices (Roder et al. 1997).

The lower regeneration of woody plants (mainly trees) and shortened swidden-fallow cycles under intensification partly explain the low diversity of spontaneous species favoured by selective weeding. While in traditional systems selective weeding has been reported to favour, i.e. not eradicate, more than 20 tree species (Denevan and Padoch 1987), in our study only 3 species were frequently mentioned by farmers. These species are either resistant to fire (*Tucumã* palm), or strong-sprouters, and can provide early harvestable products (*Envira*) or are worthy being deliberately protected by fire-breaks (Brazil nut). Fire resistance, sprouting ability and providing early-harvestable products are characteristics that allow species to persist and be managed under the current high burning frequency and short fallow cycles. Although Brazil nut can resprout and may get high enough to escape fire, farmers reported deliberate protection, whenever possible, due to its associated cultural value and its contribution to household income (also shown by Paiva et al., 2011). Therefore, under intensified conditions, selective weeding is constrained by a combination of species persistence ability and farmers valuation of its products. Although this implies that fewer useful "weeds" are managed, it also demonstrates the possibility for managing some species within an intensified system.

The increased importance of sprouting and stoloniferous species also denotes faster and more persistent graminoid infestation. As a consequence, not only more frequent weeding is needed but weeding itself becomes more laborious. Our study supports the idea that the laboriousness of weeding is related to important changes in labour and management practices (Vissoh et al. 2007). Farmers reported that weeding becomes such a toil that people are no longer willing to cooperate, so collective weeding is replaced by paid labour. But farmers who cannot afford hiring workers rely on own and close-family labour. Occasionally these farmers may not be able to handle weeds soon enough to avoid uncontrollable infestation. Rampant weed infestation is a reason given by farmers for abandoning a planted field (also reported by de Rouw, 1995). Therefore, to control weed infestation and to compensate for the back-breaking work, farmers cultivate smaller areas (Figure 5.1). Such decision partially compensates for the increased labour demand for weeding but concomitantly results in smaller cultivated area and therefore in lower household production (Figure 5.3).

Cassava yield

Cassava yield in the study area is comparable to yields reported for other swidden cultivation systems in the Amazon (Pereira and Lescure 1994, Vosti et al. 2002). However, our study also shows that cassava yield significantly decreases with agricultural intensification (Figure 5.1, Figure 5.4). After each swidden-fallow cycle cassava yield decreases 0.72 ton/ha in the absence of external inputs. A higher cassava yield at two-cycles, resulting from higher fire intensity (as explained by farmers) was also reported for other tropical regions (Styger et al. 2007), and highlights the importance of the burned vegetation for supporting yields. These results agree with previous studies showing that agricultural intensification of swidden cultivation leads to lower crop yield (Roder et al. 1997, Silva-Forsberg and Fearnside 1997, Bruun et al. 2006).

Although we could not establish a clear relation between management intensity and soil quality and between soil quality and yield, individual correlations (Table A5.1) indicated sum of bases to decrease with number of cycles (r=-0.37), and to be positively related to cassava yield (r=0.53), height (r=0.58) and basal area (r=0.64) (Table A5.1). Nutrient content in the cassava leaves, however, was not correlated to soil nutrients nor to plant size (Table A5.1). Because cassava is adapted to low-nutrient conditions, it seldom shows symptoms of nutrient deficiency in the leaves, but instead produces smaller plants and lower yields under reduced nutrient availability (Howeler and Cadavid 1983, Howeler 2001). Therefore, the decrease in cassava size (Table 5.2) strongly suggests lower overall nutrient availability after repeated swidden-fallow cycles (also reported for other crops by Roder et al., 1994, Bruun et al., 2006). These results are in accordance with reported decreased nutrient pools as a consequence of nutrient export by sequential burning, harvesting and leaching in shifting cultivation systems (Howeler 1991, Sommer et al. 2004). Such lower amounts of nutrients and intensive management practices also reduce fallow regrowth (Jakovac et al. 2015), implying that less biomass can be burned and less nutrients can support the next cropping cycle. If fallow period is shortened with intensification, nutrients released after burning could be even lower (Silva-Forsberg and Fearnside 1997, Styger et al. 2007). In our study, however, previous fallow age was not an important factor for crop yield nor weed pressure, probably due to the narrow range in fallow period in our sample and the generally short fallow periods applied in the area.

The decrease in cassava yield was probably also related to the increase in weed infestation and decrease in cassava dominance with number of cycles (Figure 5.1). Decreased cassava dominance suggests increased competition for light, which negatively affects cassava production (Howeler 2001). Hence, the decrease in cassava yield with number of cycles is a result of the increased weed competition for nutrients and light combined with reduced nutrient availability, which effects were summarized by number of cycles.

Despite the many sources of variation that can affect swidden productivity, such as fire intensity (Silva-Forsberg and Fearnside 1997), spatial distribution of laying logs (Uhl and Jordan 1984), quality of planted stalks (Embrapa 2006), and farmers strategies (Emperaire and Eloy 2015), our study shows that increasing number of cycles within a short-fallow period system has strong negative effects on swidden productivity (Figure 5.1, Figure 5.4). We show that under a short-fallow period regime, increasing the number of cycles leads to lower cassava production, higher labour demand and lower household income (Figure 5.3). If household staple supply and revenue are dependent on cassava, like in the case of the middle Amazonas region, agricultural intensification seriously threatens the sustainability of swidden agriculture. Nevertheless, the increasing *farinha* prices might be buffering the negative effects of intensification on productivity, motivating cultivation under sub-optimal conditions instead of adaptation.

Figure 5.4. Swiddens and cassava production in Central Amazon. (a) cassava field with low weed infestation; (b) cassava roots harvested from a field that was used for two swidden-fallow cycles; (c) cassava field with high weed infestation; and (d) cassava harvested from a swidden that had been more than 6 times planted

CONCLUSION

Our findings support the claim that agricultural intensification of swidden cultivation has negative socio-economic consequences, among them lower labour productivity and household income (Santley et al. 1986, Coomes et al. 2011). In our study, the transition from traditional swidden cultivation towards more modernized agriculture results in lower crop diversity and productivity without ensuing apparent benefits for farmers or the production chain. Reversing this trend requires adaptation of management practices, given that in the Amazonian villages the use of external inputs and machinery is unlikely.

Our study shows that to guarantee household sustainability in the social context of the Amazon region inevitably requires limiting the number of cycles and/or allowing longer fallow periods. Achieving this under land constraint is a challenge, but could be possible if smaller cassava fields are cultivated and higher attention is given to secondary products, as another source of income. Managing useful trees able to persist after repeated swidden-fallow cycles, such as Brazil nut and Tucumã, would allow additional profits during both fallow and cropping periods. Decreasing household reliance on cassava and diversifying production did boost the sustainability of swidden cultivation in the Amazon (Pereira and Lescure 1994). Finally, given that agricultural intensification is likely to become reality in many traditional communities, learning how local people are coping with intensification pressure in different areas will help to foster realistic adaptation strategies.

ACKNOWLEDGMENTS

The authors are grateful to the inhabitants of the villages Vila Sião, São Francisco, Jauarituba, Monte Carmelo and Agrovila who authorized and contributed to this research. We are thankful to Reney Falcão for assistance during field work and to Mr. Falcão and Mr. Ilson families for kindly hosting the field expeditions. We also thank the Instituto Chico Mendes de Conservação da Biodiversidade for authorizing research in the National Forest Reserve FLONA Tefé and for logistic support in the field. This research was funded by The Netherlands Fellowship Program (NFP-NUFFIC). The first author received scholarships from Wageningen University (NL) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (Br) through the Instituto Nacional de Serviços Ambientais da Amazônia – SERVAMB. This research is in accordance with the Brazilian regulation on ethics in research, under project number 20361713.7.0000.0006, approved by the Comissão Nacional de Ética em Pesquisa-CONEP and Comitê de Ética em Pesquisa from the Instituto Nacional de Pesquisas da Amazônia (Br).

APENDIX 5

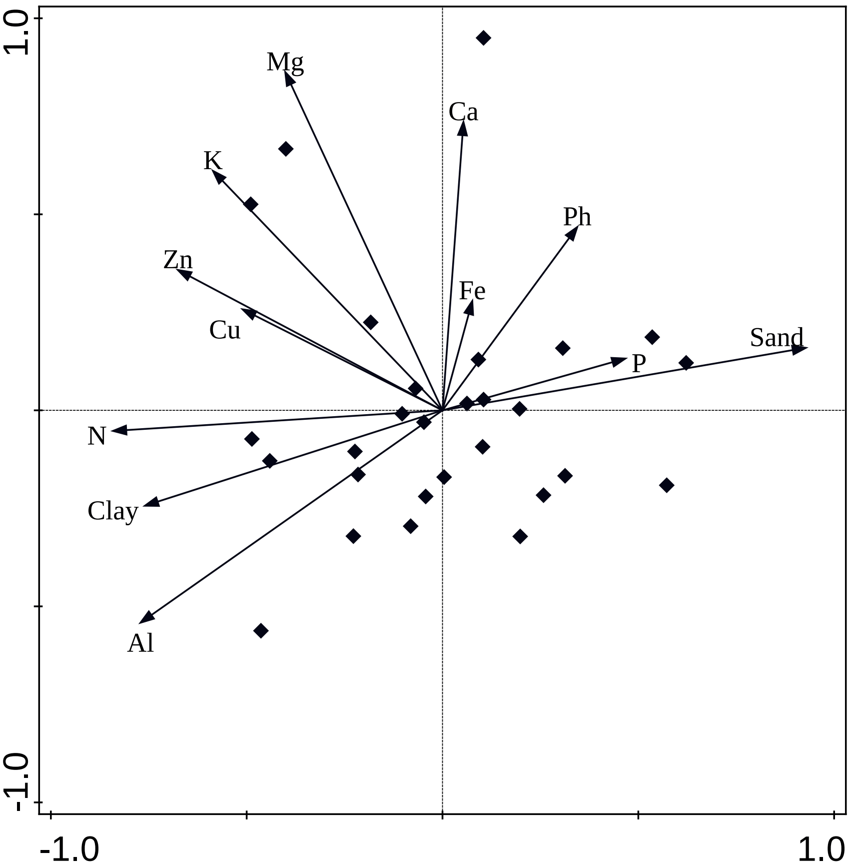


Figure A5.1. Ordination of soil properties of swiddens from Central Amazon, Brazil. Principal Component Analysis of soil chemical and physical properties of 28 swiddens surveyed in 2013. The first two axes explain 55.5% of variation, with 31.8% explained by the first axis and 23.7% by the second axis.

Table A5.1. Correlation table of variables describing management practices, soil properties, cassava development and yield in 28 swiddens located at the region of the middle Amazonas river, Tefé, Brazil.

	Management				*Soil properties*																	*Leaf nutrient*					*Cassava development*		
	Number of cycles	Previous fallow age	Weeding effort	Post-planting time	Silt	Sand	Clay	pH	C	N	P	K	Ca	Mg	Al	SB	CEC	Fe	Zn	Mn	Cu	N	P	K	Ca	Mg	Cassava density	Fresh-root weight	Cassava height
Management																													
Number of cycles	1.00																												
Previous fallow age	-0.24	1.00																											
Weeding effort	0.24	-0.23	1.00																										
Post-planting period	0.09	-0.05	0.42	1.00																									
Soil properties																													
Silt	0.03	0.05	0.05	0.24	1.00																								
Sand	0.20	-0.13	-0.07	-0.14	-0.88	1.00																							
Clay	-0.47	0.19	0.06	-0.09	0.27	-0.69	1.00																						
pH	-0.25	-0.12	0.04	0.16	-0.19	0.26	-0.24	1.00																					
C	-0.05	0.04	0.01	0.16	0.60	-0.52	0.14	-0.25	1.00																				
N	-0.14	0.24	0.04	0.13	0.76	-0.79	0.45	-0.32	0.89	1.00																			
P	-0.13	-0.11	-0.27	-0.26	-0.42	0.54	-0.47	0.08	0.14	-0.19	1.00																		
K	-0.28	-0.07	0.11	-0.01	0.39	-0.38	0.18	0.06	0.48	0.47	-0.15	1.00																	
Ca	-0.21	0.04	0.01	-0.04	-0.14	0.15	-0.09	0.21	-0.08	-0.08	0.06	0.22	1.00																
Mg	-0.42	0.11	-0.02	-0.16	0.19	-0.21	0.14	0.18	0.23	0.26	-0.05	0.71	0.70	1.00															
Al	-0.15	0.14	0.14	0.15	0.63	-0.84	0.75	-0.46	0.41	0.68	-0.37	0.08	-0.32	-0.15	1.00														
SB	-0.37	0.06	0.02	-0.10	0.11	-0.12	0.07	0.19	0.18	0.19	-0.02	0.66	0.85	0.96	-0.20	1.00													
CEC	-0.23	0.15	0.15	0.14	0.67	-0.89	0.78	-0.43	0.46	0.73	-0.38	0.21	-0.16	0.05	0.98	0.00	1.00												
Fe	0.00	0.03	-0.29	0.13	0.22	-0.07	-0.21	0.27	-0.34	-0.19	-0.35	-0.01	0.18	0.09	-0.17	0.12	-0.14	1.00											
Zn	-0.32	0.31	0.07	0.17	0.63	-0.56	0.18	-0.01	0.69	0.72	0.02	0.63	0.05	0.50	0.33	0.41	0.42	-0.02	1.00										
Mn	-0.32	0.19	0.03	-0.27	-0.16	0.00	0.25	0.20	-0.10	-0.02	-0.03	0.39	0.67	0.77	-0.19	0.77	-0.03	-0.02	0.17	1.00									
Cu	-0.25	-0.12	-0.10	-0.33	0.19	-0.36	0.43	-0.26	0.10	0.17	-0.26	0.44	0.02	0.44	0.10	0.32	0.17	0.08	0.25	0.35	1.00								
Leaf nutrient																													
N	0.02	0.13	-0.04	-0.20	-0.32	0.36	-0.26	0.04	-0.06	-0.16	0.28	0.00	0.20	0.17	-0.47	0.18	-0.44	-0.05	-0.01	0.27	0.16	1.00							
P	-0.09	0.09	0.09	-0.28	-0.06	0.00	0.10	0.02	0.17	0.13	0.21	0.24	0.13	0.27	-0.07	0.25	-0.03	-0.32	0.18	0.46	0.18	0.53	1.00						
K	0.02	0.00	-0.03	-0.28	-0.12	0.13	-0.07	-0.17	-0.03	-0.06	0.03	0.35	0.08	0.18	-0.24	0.20	-0.20	0.00	0.15	0.23	0.39	0.31	0.46	1.00					
Ca	0.02	-0.11	-0.29	0.03	-0.29	0.24	-0.06	0.43	-0.35	-0.37	-0.03	-0.32	0.37	0.02	-0.29	0.11	-0.27	0.21	-0.46	0.14	-0.19	0.02	-0.36	-0.48	1.00				
Mg	0.01	0.04	-0.05	0.08	0.49	-0.32	-0.09	0.34	0.50	0.41	0.02	0.28	-0.24	0.09	0.03	-0.01	0.03	0.10	0.53	-0.11	0.20	0.08	0.25	0.19	-0.26	1.00			
Cassava development																													
Cassava density	-0.03	-0.01	0.06	-0.24	-0.16	0.05	0.14	-0.15	-0.23	-0.17	0.09	-0.20	0.13	-0.09	0.05	-0.03	0.04	0.10	-0.12	0.25	0.28	0.36	0.45	0.33	-0.13	0.01	1.00		
Fresh-root weight	-0.50	0.17	-0.11	0.07	0.02	-0.07	0.11	0.25	0.26	0.23	0.11	0.38	0.47	0.48	-0.03	0.53	0.08	-0.04	0.17	0.30	-0.13	-0.01	0.17	-0.14	0.23	-0.08	-0.27	1.00	
Cassava height	-0.60	0.04	0.06	0.11	0.23	-0.37	0.41	0.22	0.17	0.30	-0.25	0.36	0.52	0.56	0.21	0.58	0.33	0.14	0.20	0.35	0.15	-0.01	0.03	-0.20	0.26	-0.05	-0.10	0.69	1.00
Cassava basal area	-0.73	0.08	-0.06	-0.12	0.11	-0.34	0.52	0.24	0.24	0.32	0.00	0.46	0.45	0.67	0.19	0.64	0.33	-0.14	0.32	0.50	0.25	0.03	0.30	0.00	0.11	0.01	-0.11	0.72	0.85

Chapter 6

General discussion

Catarina C. Jakovac

Reconciling human needs while conserving ecosystems and the benefits they provide is an increasing challenge. In the search for an equilibrium between agricultural productivity and ecosystem integrity, it is important to understand how resilient agricultural systems and forests are to different types and intensities of land use. In the tropics, swidden cultivation is the traditional land-use system that supports livelihoods and transforms landscapes. In the last decades, swidden cultivation is undergoing pressure for transition towards agricultural intensification, and is experiencing important changes in the way the agro-ecosystems are managed. Agricultural intensification is the process of shortening the fallow period and increasing the frequency of swidden-fallow cycles in the same area.

The aim of this thesis was to evaluate the consequences of agricultural intensification for the resilience of the socio-ecological system around the production of cassava in riverine communities of the Brazilian Amazon. Resilience is the capacity of socio and ecological systems to absorb disturbance and still retain the same function and structure, as well as the capacity to self-organize and adapt in the face of perturbations and crises (Berkes et al. 2002). The results of this study show that constraints of land accessibility combined with socio-economic drivers pushed the system towards agricultural intensification in the last three decades, leading to a landscape currently dominated by young secondary forests (< 10 years, Chapter 2). At the field level, agricultural intensification reduced the recovery capacity of secondary forests (Chapter 3 and 4) and the labour productivity of swiddens (Chapter 5). Along with agricultural intensification, market integration led to lower crop and landraces diversity and simplified management practices (Chapter 5).

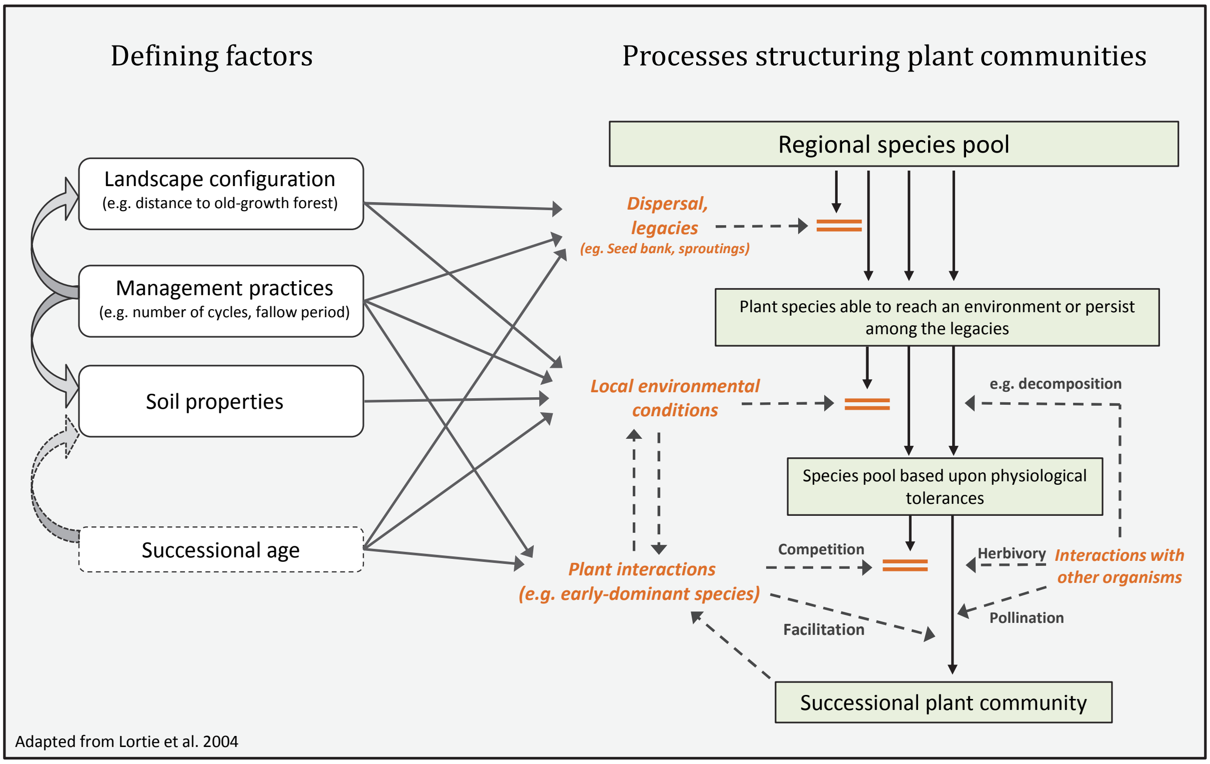
By integrating these main findings, in this general discussion I evaluate the consequences of agricultural intensification for the resilience of the socio-ecological system. First, I discuss how the recovery of secondary forests is affected by land use, and reflect on the possible consequences for ecosystem functioning. Next, I discuss how management practices are changing along with swiddens productivity and assess farmers ecological knowledge to identify management-environment feedbacks and thresholds of system change. Considering the context of riverine Amazonia, I provide recommendations to revert this trend, focusing on the management of fallows for fostering multifunctional landscapes and increase the possibilities for adaptation. Finally, I reflect on the challenges and opportunities of the *farinha* market for riverine communities, and conclude with the main messages from this thesis.

PROCESSES STRUCTURING PLANT COMMUNITIES IN HUMAN-MODIFIED LANDSCAPES

Secondary forests are important components of human-modified landscapes. Secondary forests, however, are not a homogeneous category as they follow different successional trajectories depending on previous land-use history (Mesquita et al. 2001, Slocum 2001, Hooper et al. 2004, Walker et al. 2010a). The relation between land use and forest succession is, however, complex, because land-use effects are actually mediated by concomitant impacts of management practices, landscape configuration, and site conditions. Given that most secondary forests regrow after land use, to advance the knowledge on tropical forest succession, it is important to understand how human-driven factors affect successional communities.

The results of this thesis indicate that ecological filtering processes play an important role in mediating the effect of land use on successional communities (Chapter 4). Land-use related factors act on species characteristics selecting for suitable traits that pass the different biotic and abiotic filters (Keddy 1992). Based on the hierarchical basis of succession (Pickett et al. 1987) and community assembly theories (Grime 1998, Lortie et al. 2004), I adapted the conceptual framework of Lortie et al. (2004) to the results of this thesis to discuss how successional communities are structured in human-modified landscapes. In this framework, successional communities are the product of three main filtering processes acting on species availability (dispersal and legacies), establishment success (local environmental conditions) and species performance (plant-plant and plant-other organism interactions) (Figure 6.1). In human-modified landscapes these three filtering processes are defined by four main factors: landscape configuration, management practices, soil properties and successional age. In this thesis I evaluated the effects of the first three factors on early successional communities.

The relative importance of landscape configuration, management practices and soil properties on successional communities vary with land-use context and successional age (Chazdon 2008). At early stages of succession the impacts of those factors can be more clearly depicted than further on, when changing microclimatic conditions in the understory (Lebrija-Trejos et al. 2011, Lasky et al. 2014, Lohbeck et al. 2014), and plant-plant interactions (van Breugel et al. 2011) may override initial differences related to land use. A frequent limitation of chronosequence studies is the inability to differentiate direct effects of land use, e.g. management practices, from indirect effects, such as those mediated by the established vegetation (Norden et al. 2011, Jakovac et al. 2014, Williamson et al. 2014). The sampling design used in this thesis, in which I excluded the effect of successional age and focused on the early stages of succession, allowed to elucidate how direct land-use factors define the structure and species composition of early-successional communities.



Adapted from Lortie et al. 2004

Figure 6.1. The main processes or filters that structure successional communities (to the right) and the external factors affecting it in the context of human-modified landscapes (to the left). Each process/filter is represented by a pair of horizontal lines, with the corresponding description in italic (sub-sets of a process such as herbivory or competition are labelled in plain text). Solid vertical black arrows depict the movement of species through the filters, and hatched lines illustrate where each process might influence the plant community. Solid grey arrows indicate how external factors affect these processes and therefore the structuring of successional plant communities. The factors not studied in this thesis are enclosed in a dashed box. This diagram was modified from Lortie et al. 2004.

I showed that at early stages of succession, management practices have a stronger effect on vegetation structure and species composition than landscape configuration and soil properties (Chapters 3 and 4). Management practices were the most important factors determining the life-forms that first colonize fields (represented by weeds regenerating in swiddens; Chapter 5), as well as the vegetation structure (Chapter 3) and species composition of early tree communities (Chapter 4). Cutting and burning practices act upon the legacies left after disturbance (Figure 6.1), by gradually eliminating seed-dependent species and selecting for species able to resprout repeatedly (Chapter 2 and 4). Fire resistant seeds may also be favoured (Hooper et al. 2004). Such selection determines the identity of the dominant species, and narrows down the set of species present in the community, reducing the species alpha and beta diversities (Chapter 4). When diversity is low and regeneration depends mainly on resprouters, diversification during succession will rely 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, Cubiña and Aide 2001, Wieland et al. 2011) and the position of intensively used sites in fragmented and deforested landscapes (Robiglio and Sinclair 2011), species build-up is bound to be slow after intensive land use. Therefore, the great impact of management practices on the legacies, and on the early stages of succession can last for long time and can be largely responsible for arresting succession. These results help explain divergent successional pathways following high land-use intensity reported for other areas of the Amazon (Mesquita et al. 2001, Williamson et al. 2014).

Management practices also affect successional communities through altered soil conditions (Figure 6.1, left side). After repeated nutrient losses by burning and cropping, soil fertility is reduced (Chapters 3 and 4, Uhl and Jordan, 1984). Such reduction could not be clearly detected in the soils of secondary forests (Chapter 3), probably because nutrients released to the soil after burning are rapidly up-taken by the vegetation or adsorbed to clay particles and metal (hydr-)oxides, returning to similar low levels found in old-growth forests within 2 to 7 years after abandonment (Nye and Greenland 1964). Nonetheless, reduced fertility could be detected in the cropping fields (Chapter 5), measured as a decrease in the amount of basic cations, which actually corresponds to the nutrients made available by burning the secondary forests biomass. Moreover, reduced fertility was also evidenced through the lower cassava development and yield (Chapter 5), and lower basal area and canopy height of fallows (Chapter 3). Finally, using a non-linear analysis, it was possible to identify associations between low phosphorus availability and intensive land-use, which were also related to the identity of the dominant species on secondary forests (Figure 4.1, Chapter 4). This result agrees with other studies showing a reduction in phosphorus availability with land use (Runyan et al. 2012), and corroborates its role in determining species distribution in tropical forests (John et al. 2007, Toledo et al. 2012, Condit et al. 2013). Nevertheless, limitations of this study in detecting clear patterns associated with soil, were probably related to the assessment of static soil conditions, which has been the usual procedure in ecological assessments (Buschbacher et al. 1988, Feldpausch et al. 2004, Ribeiro Filho et al. 2013), and may not give a clear picture of actual nutrient dynamics (e.g. Broadbent et al. 2014). Future research should invest in estimations of nutrient fluxes to clarify the role of soils on succession.

Land use inevitably change landscape configuration through the reduction of old-growth forests cover, forest fragmentation, and the expansion of young secondary forests, as well as the creation of agricultural lands (Lawrence et al. 1998, Metzger 2002, van Breugel et al. 2013). By decreasing the cover by old-growth forests, which are the sources of seeds to secondary forests, species dispersal limitation is strengthened (Figure 6.1) and therefore, the range of species able to reach open sites may be reduced (Robiglio and Sinclair 2011, Chapter 3). Corroborating other studies, I found that landscape configuration played a secondary role at early stages of succession, contributing to the species richness of mainly young saplings and not affecting species composition of early pioneer species (Chapter 4, Guariguata et al. 1997, Holl et al. 2000, Benítez-Malvido et al. 2005). These findings suggest that landscape configuration may have a more important effect on species turnover at advanced stages of succession than at earlier stages. Under high land-use intensity, landscapes may become dominated by young secondary forests, as happened in the study area (< 10 years old; Chapter 2), reducing the chances of long-living tree species to perpetuate in the landscape (van Breugel et al. 2013). Therefore, secondary forests enclosed in simplified landscapes will have reduced capacity to diversify, and species turnover will be mainly dependent on the legacies left after disturbance, or on restoration actions.

This study have shown that land use determined the identity of early-dominant species by selecting for specific traits (Figure 6.1). This early vegetation will further regulate environmental conditions in the understory (Kabakoff and Chazdon 1996, Lebrija-Trejos et al. 2011, Jakovac et al. 2014), important biotic interactions (Walker et al. 2010a, Maggi et al. 2011) and ecosystem functioning, such as litter decomposition (Carreño-Rocabado et al. 2012) during the first decades of succession (Finegan 1996, Longworth et al. 2014). To disentangle the direct and indirect effects of land use on the development of successional communities in alternative pathways, field experiments should investigate the role of plant-plant interactions (Figure 6.1) on successional processes following different land-use intensities.

The results of this thesis are based on shifting cultivation practices, but the processes through which land use affects succession might be similar in other land use systems common in the tropics. Pasture lands in the Amazon are also managed by prescribed burning and also generate secondary forests with poor seed bank (Mônaco et al. 2003) and dominated by similar species, such as *Vismia* and *Bellucia* (Mesquita et al. 2001, Chapter 4). The adapted conceptual framework based on filtering effects used in this discussion can, therefore, provide the basis for further development of a conceptual model that describes succession in human-transformed landscapes in the tropics.

Land-use effects on ecosystem functioning

I showed that land-use filtering effects induces a shift in species composition (Chapter 4). Such shift was intimately associated with the selection for a specific trait: sprout ability (Chapters 3 and 4), which is usually associated with other plant traits such as growth rate (Figure 6.2, Figure 6.3). Although early secondary forests are generally dominated by acquisitive pioneer species (Finegan 1996), these species may vary in growth strategies and rate, as well as in the quantity and quality of the nutrients they accumulate (Uhl 1987, Gomes and Luizão 2012, Broadbent et al. 2014). Therefore, the selection for sprouting trait possibly also implies in changes in ecosystem functioning.

In the shifting cultivation system studied, management practices of cutting, burning and weeding practices induced a shift in species composition through the selection for strong-sprouters (Chapters 3 and 4). Although most tropical forest species are able to resprout (Kauffman 1991, Poorter et al. 2010), only a few can resprout after losing its aboveground biomass repeatedly (Bond and Midgley 2001, Hooper et al. 2004). These strong sprouters are usually slow growers, because there is a trade-off between investing in growth or in below-ground storage (Bond and Midgley 2001, Poorter et al. 2010). Corroborating this idea, I have identified a correlation between the sprout ability of species and their average and maximum height after five years of succession (Figure 6.2). Also, I identified that a seed-dependent species (*Cecropia sciadophylla*) was usually taller than a strong-sprouter species (*Vismia cayannensis*) after 5 years of succession (Figure 6.3). These two species dominate at the two extremes of the land-use intensity gradient (Chapter 4), and also differ in other functional traits.

Vismia cayannensis has higher sprout ability, slower growth rate, higher wood density, lower leaf nutrient concentrations, higher leaf longevity and longer generation time, when compared to the dominant species at low land-use intensity levels, *Cecropia sciadophylla* (Gomes and Luizão 2012). High wood density, high leaf longevity and low nutrient concentration are mechanisms associated with resource conservation, defence and survival (Aerts 1990, Escudero et al. 1992, Reich et al. 1995), and probably confer advantages for species colonizing sites where soil conditions are less favourable (Chapter 3 and 4). Within the functional traits spectrum of tropical forests, these species would be classified as acquisitive species (Poorter and Bongers 2006). But this and other studies suggest that these pioneer species may represent a range of strategies related to colonization and survival, which could form a fast-slow spectrum within pioneer species (Reich and Cornelissen 2014).

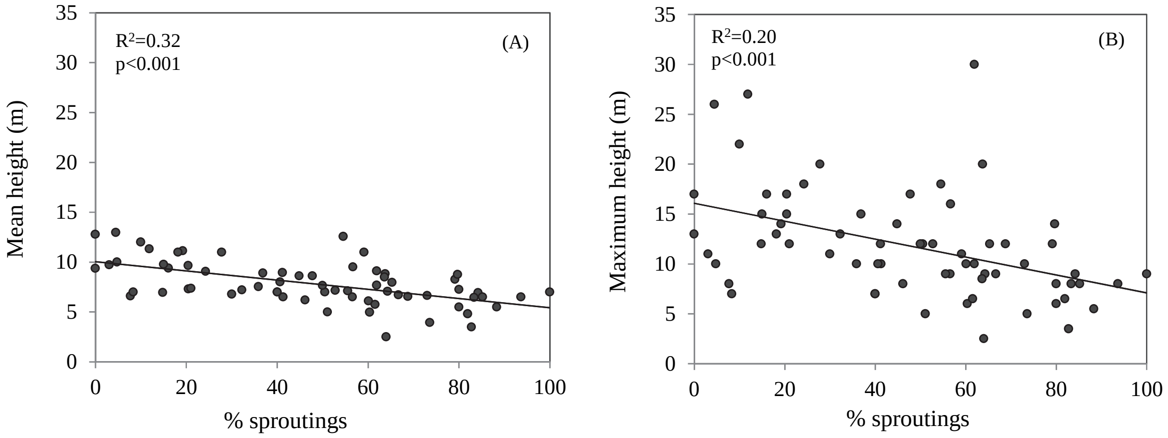


Figure 6.2. Relation between species mean (A) and maximum (B) height and percentage of sproutings. Percentage of sprouting was calculated as the percentage of individuals of that species found sprouting in the whole database. Each point in the graph is a species, and only species with > 10 individuals with DBH> 5 cm sampled were included.

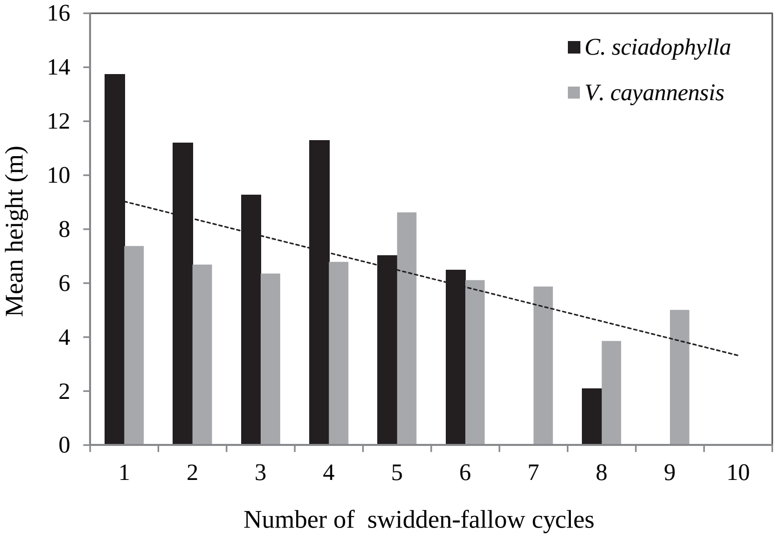


Figure 6.3. Mean height of Cecropia sciadophylla and Vismia cayannensis along a gradient of land use intensity. Mean height was calculated only for non-sprouting individuals with dbh > 5 cm (to control for possible effects of “sprouting exhaustion” on growth and possible differences between seedlings and sproutings growth rates), in secondary forests subjected to different number of cycles. Dashed trend line represents the mean canopy height of secondary-forest stands at different levels of land-use intensity.

In successional forests, where dominance is high, the dominant species largely determine ecosystem functioning (Lohbeck 2014), and therefore variations in their functional traits could be up scaled to ecosystem functioning (Suding et al. 2008). The survival traits that characterize a “slow” strategy may promote slow nutrient cycling and low rate of microclimate transformation in the understory. These two processes are important aspects on which successional processes and species turnover depend (Denslow and Guzman 2000, van Breugel et al. 2006). Low leaf nutrient content means lower decomposition rate and, together with low leaf turnover, results in low carbon and nutrient cycling in the system (Reich and Cornelissen 2014) and consequently, slower soil amendment during succession. Moreover, the combination of slow growth rates and low plant height result in stands with short canopy and high light availability in the understory (Jakovac et al. 2014, Jakovac et al. 2015), possibly favouring pioneers over shade-tolerant species and delaying species turnover. Therefore, the dominance by species with 'slow' traits at early stages of succession might promote low ecosystem dynamics, and contribute to trap the system in an arrested successional stage. This indicates a positive feedback where plant communities emerging at high intensity of use are less efficient in restoring ecosystem functions.

Elucidating the relation between land use and ecosystem functioning is a key to understand how land-use systems affect the resilience of secondary forests. Future research should investigate the idea that slow ecosystem dynamics result from high land-use intensity. Additionally, re-classifying pioneer species in a fast-slow spectrum, including leaf, stem and root traits, will help understand how functional traits of early successional species and biogeochemical cycles change along gradients of land-use intensity. Controlling for successional age would be desired in a trait-based analysis, to avoid confounding patterns actually related to the strong effect of other changing conditions during succession, such as light availability (Poorter and Bongers 2006, Carreño-Rocabado et al. 2012). A trait-based approach will be helpful to optimize management (Brussaard et al. 2010, Diaz et al. 2011), and to improve the ability of fallows to provide the aimed ecosystem services.

THE SOCIO-ECOLOGICAL SYSTEM UNDER TRANSITION

In the last four decades, riverine Amazonia has been experiencing important changes in its socio-economy and demography (Brondizio 2009), with rapid urbanization and increased demographic concentration around villages and around the local urban centres (Padoch et al. 2008, Parry et al. 2010a, Eloy 2015). Such processes usually result in transformations in the patterns of resource use (Brondizio et al. 1994). In one hand, such transformations may open windows of opportunity for traditional products (Brondizio et al. 1994, Brondizio 2009) but on the other can lead to negative effects for people and the environment (Sirén 2007). While in many agricultural frontiers swiddens are being replaced for permanent agriculture and the staple food is giving place to cash crops or pasturelands (Padoch et al. 2007, Rerkasem et al. 2009, Ziegler et al. 2009, van Vliet et al. 2012), in the study area, swidden agriculture is integrating to the market by means of the traditional crop, cassava. Nevertheless, the results of this thesis show that swidden cultivation in the region of the middle-Amazonas river is going through transformations related to agricultural intensification (Chapter 2) that may have negative effects for the system (Chapters 3, 4 and 5).

In the Brazilian Amazon, the increasing urban population and out-migration from rural areas (Parry et al. 2010a) is resulting in higher demand for *farinha* along with increasing prices (Chapter 2). High market demand has made *farinha* the easiest and most convenient product to be sold, because a network of middlemen has established at virtually every riverine village (Pereira et al. 2008, Brondizio 2009, Lima et al. 2012). Farmers have reported that selling *farinha* is more convenient nowadays because they do not need to handle the costs of travelling to and staying at the cities for selling the produce. While this middlemen network frees farmers from high transportation costs, it also imposes a product monopoly.

The high demand for *farinha* and trading convenience has increased farmers' focus on cassava as a single main crop, transforming the system towards simplified management practices and reduced crops and landraces diversity when compared to other traditional systems (Chapter 5, Pereira and Lescure 1994). In the last 10 years a new variety, called *catombo*, emerged and rapidly spread around, currently dominating virtually every swidden in the region of the middle-Amazonas river (Lima et al. 2012, Chapter 5). Reduced crop diversity and increased dominance have been reported for swiddens elsewhere in the Amazon (Peroni and Hanazaki 2002, Lima et al. 2012, Kawa et al. 2013). The loss of landraces, and possibly the knowledge associated with experimentation and diversification (Emperaire and Eloy 2015), increases the susceptibility of production systems to pest outbreaks and to changing environmental and social conditions (Cavechia et al. 2014). Such feedbacks work against the resilience of the socio-ecological system, by decreasing the possibilities for diversification. Additionally, the restricted market opportunities do not encourage diversification and restrain the possibilities for adaptation.

Management-environment interactions

I showed that in the last three decades, the fallow period in the study area has decreased throughout the studied landscape and the frequency of swidden-fallow cycles has increased, characterizing an intensification process (Chapter 2). Within the current short-fallow-period regime, increasing the number of swidden-fallow cycles results in a decrease in fallow recovery capacity and swiddens productivity (Chapters 3, 4 and 5). The overriding importance of number of cycles relies on the fact that it summarizes a number of synchronic changes and feedbacks that enhance the actual impact of cutting and burning practices.

With number of cycles, recovery rate decreased, liana infestation and percentage of resprouts increased (Fig. 4, Chapter 3) and species composition changed (Chapter 4). Swiddens showed a decrease in crop productivity and a change in weeds life-form composition and infestation rate (Chapter 5). Number of cycles also resulted in changes in soil properties, such as pH, clay content, sum of bases and P availability (Chapters 3, 4 and 5). These simultaneous changes in different components of the system interact and reinforce the effect of cutting and burning practices (number of cycles) on the swidden-fallow system.

Likewise, there is an interplay between farmers management practices and the environmental and biotic conditions. In response to increased weeds infestation, farmers increased the frequency of weeding (Chapter 5). Clean-weeding practices, which are based on pulling and cutting off virtually every spontaneous plants, helps impoverishing the seed bank and favours the persistence of strong-sprouter species (de Rouw 1993). Strong sprouters are hard-to-weed (Staver 1991) and are slow growers (Figure 6.2) that will give place to slow-growing secondary forests with limited potential to fertilize the next cropping cycle and to suppress weeds. Such management-environment interactions represent feedbacks that enhance the negative effects of intensification on the resilience of the socio-ecological system. If there is interest in enhancing the resilience of the system, these feedbacks would need to be broken.

Tired lands: threshold for managing resilience

Identifying thresholds offer a means to quantify how much disturbance an ecosystem can absorb before switching to another state, and indicate whether and when intervention might be necessary to promote the recovery of the pre-disturbance state (Standish et al. 2014). In this study, along a gradient of agricultural intensification, the system showed gradual changes towards slower recovering rates of fallows (Chapter 3) and lower productivity of swiddens (Chapter 5), rather than a sudden flip to a different state. Nevertheless, the integrated perception of farmers upon the system suggests the formation of *tired lands* to be a threshold for managing resilience.

Farmers associate repeated swidden-fallow cycles with the formation of "*tired lands*" (*terras cansadas*, in Portuguese). *Tired lands* are consensually characterized by farmers in three interrelated aspects: low yield, high weed pressure and slow fallow growth. To identify the threshold when a field would be considered tired, I walked with farmers through their fields asking whether specific fields were a *tired land* or not (n=107 fields questioned, 40 farmers interviewed), and queried about the land-use history of that field. According to farmers' answers, the probability of a field been considered "*tired*" reaches 90% after 4 swidden-fallow cycles ($P < 0.001$, DF=105; Figure 6.4). This threshold coincides with the verge of number of cycles where important changes were detected in the species composition and soil quality of secondary forests (Chapter 4, Figure 4.1). This threshold also coincides with system transitions reported for swidden cultivation systems elsewhere (Styger et al. 2007). When a field is close to or has become *tired*, farmers would allow longer fallow period or would implement agroforestry systems. Monitoring the state of resources is a mechanism for managing resilience present in many socio-ecological systems (Berkes et al. 2002), where by identifying ecosystem changes through ecological knowledge, people may prevent the build-up of large-scale crises.

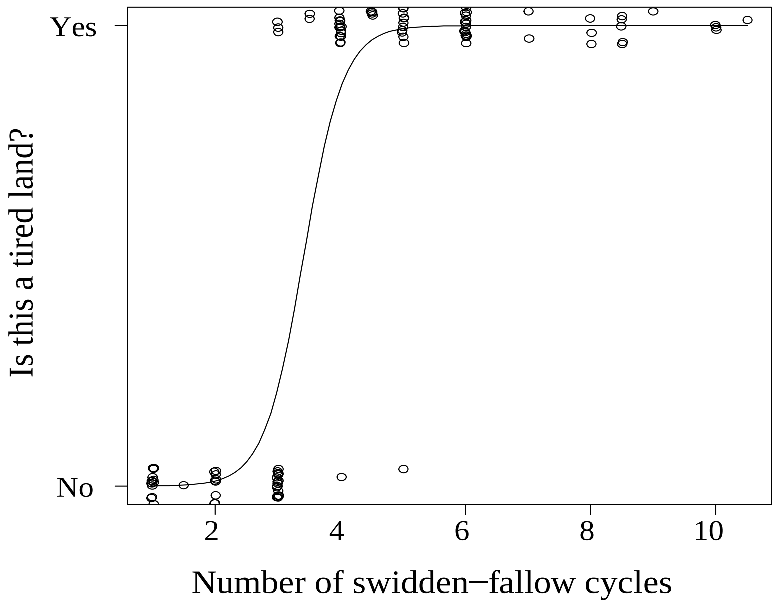


Figure 6.4. Logistic regression applied to farmers answer (yes=1 or no=0) to the question "Is this a *tired land*?" (estimate=3.15±0.7, p<0.001, DF= 105). Interviews were done during walking transects with 40 farmers in seven communities of the middle-Amazonas river, Brazil. Each dot represent an agricultural field (N=107).

When land is scarce, however, farmers may decide to keep on cultivating on these *tired lands* (Chapter 2 and 5). Cassava, and especially bitter cassava, is a crop well adapted to low nutrient availability, being able to grow and yield on poor and acid soils (Chapter 5, Howeler et al. 2001). I showed that swiddens that underwent ca. 10 cycles still yield ca. 10 tons of fresh-root cassava per hectare, against the overall mean of 15 ton ha^{-1} (Figure 5.1, Chapter 5). In this sense, cassava may guarantee resilience to livelihoods, allowing production where no other crop would do (Howeler 2001). However, by postponing the abandonment of *tired lands*, continued cultivation further reduces the recovery capacity of fallows and may push it into an arrested succession state (Chapters 3 and 4). In systems strongly dependent on natural recovery, with no use of external inputs, as most riverine communities in the Amazon, threatening the recovery capacity of the system jeopardizes its resilience. In the current social context, the increasing prices of *farinha* might buffer the negative effects of intensification on production, motivating farmers to carry on cultivation on *tired lands*. Therefore, the combination of land constraint, a low-nutrient requiring crop, and better *farinha* prices, might be pushing the system over its safe threshold.

Currently, most of the landscape still did not reach the *tired land* threshold (80% of the fields had experienced < 4 cycles; Chapter 2). However, with the current limitation for swiddens expansion and the general short fallow periods practiced in the region (Chapter 2), *tired lands* will likely expand if current practices are maintained. Once the *farinha* market is no longer profitable, a footprint of *tired lands* will allow low adaptability and will require costly reversion of ecological resilience. Whether the system will cross this safe threshold towards the "collapse" or will adapt before that, is rather unpredictable due to the complexity of factors in play, such as policies, knowledge and environmental conditions. Riverine communities in the Amazon have shown high adaptability to market fluctuations, guaranteed by the maintenance of a heterogeneous landscape and a diversity of land-use systems (Vogt et al. 2015). In this study I have focused only on cassava cultivation, which is the main land-use system and the one suffering major changes. Other economic activities, such as fishing, harvesting of Brazil-nut and off-farm labour, may however gain importance and allow other means of adaptation. The adaptation pathway to be navigated will largely depend on opportunities created by institutions related to the production system (Vogt et al. 2015).

RECOMMENDATIONS TOWARDS MULTI-SERVICE LANDSCAPES

To improve the sustainability of swidden cultivation systems several alternatives have already been proposed (Vosti et al. 2002, Denich et al. 2005). Nevertheless, few of those have been adopted by farmers because, among other reasons, many alternatives require substantial transformations in the system and therefore demand close and long-term presence of technical assistance institutions (Pollini 2009). Given the difficulties of having the presence of such institutions for long-term, alternatives originated on farm or brought about in participatory discussions are more widely adopted (Pollini 2009). Moreover, the success of alternatives is dependent on social and environmental constraints (Cairns 2015), requiring that recommendations be contextualized. Therefore the following recommendations are brought forward on the basis of trade-offs between costs and opportunities within the context of riverine Amazon (Chapter 1, Chapter 5).

To decrease the nutrient losses in swidden cultivation systems, fire-free alternatives have been widely proposed but, due to several drawbacks, have rarely been adopted by farmers (Szott et al. 1999, Lojka et al. 2008). For example, slash-and-mulch was shown to reduce nutrient losses (Sommer et al. 2004, Denich et al. 2005) but also to increase labour costs for managing the field (including clearing and weeding) (Norgrove and Hauser 2015) and to reduce crop yield in the short term (Kato et al. 1999, Lojka et al. 2008). On poor acid soils, fire is an important tool for short-term soil fertilization, as well as for clearing logs and branches and delaying weed infestation (de Rouw 1995, Kleinman et al. 1995). On low input systems, fire-free alternatives are unlikely to be adopted by farmers.

In the context of riverine Amazon, where access to technology and technical assistance is low, mechanization and use of fertilizers would increase the vulnerability of the socio-ecological system to environmental degradation and external crises (Bruun et al. 2009, Rerkasem et al. 2009, Ziegler et al. 2009). The strength of riverine areas is undoubtedly related to the availability of natural resources and the associated ecological knowledge (Sears et al. 2007, Vogt et al. 2015). Swidden cultivation has been shown to be productive when agriculture and forest products are not segregated (Castella et al. 2013). Therefore, my recommendations point towards improving the sustainability of cassava cultivation but also fostering multifunctional landscapes.

Adapting management practices

This thesis have shown that swidden cultivation is unsustainable when many swidden-fallow cycles are alternated with short fallow periods (≤ 5 yrs), and when regrowth depends exclusively on natural regeneration (Chapter 5). Ideally, with increasing number of cycles in the same area, longer fallow periods would be required to achieve similar crop yields. Additionally, the threshold of *tired lands* should be respected and the use of the same field for more than four swidden-fallow cycles should be avoided in a short-fallow-period regime. However, this may not be feasible under conditions of land constraint and when livelihoods rely strongly on cropping. One option to allow longer fallow periods under land constraint is to cultivate smaller fields. This could be fostered by sharing income between cassava and fallow products. Additionally, practices to accelerate the recovery of secondary forests could provide a transition to a more resilient landscape.

Fallows can be managed for different purposes, such as improved fallows for soil fertility or enriched fallows for providing products. Improved fallows for soil fertility consists of planting or favouring trees for improving biomass accumulation of fallows and availability of nutrients for the next cropping period (Kanmegne et al. 1999, Lojka et al. 2008, Marquardt et al. 2012). Improved fallows with N-fixing plants have been shown to enhance crop yield in N-limited environments (e.g. Lojka et al. 2008). On phosphorus-limited soils, however, N-improved fallows must be complemented with P fertilization (Szott et al. 1999). On the poor and acid soils of the Amazon, where the concentration of several nutrients is generally low (Chapter 5), cassava yield could be enhanced through the cutting and burning of fallows with higher amounts of biomass (Szott et al. 1999). Favouring fast-growing species and controlling strong-sprouters by girdling and shading can speed up vegetation recovery (Ramakrishnan and Toky 1981). Studies have shown that cassava development is enhanced when fields are kept weed-cleaned in the first 70 days post-planting (Embrapa 2006). After this period, which usually represents the 2nd and 3rd weeding events, fast-growing trees such as *Cecropia* spp., *Jacaranda copaia* and *Inga* spp., could be left sparsely on swiddens or could be sowed during the final moments of the cropping period.

Enriched fallows can be a source of agroforest products. Tree species that provide timber and fruits could be managed on fallows or across the landscape surrounding swiddens. Enriched fallows have been a common practice in the past (Denevan and Padoch 1987, Dalle and de Blois 2006) and can complement farmers income. Fruits, nuts and timber trees could be managed within not-that-long fallow periods (10 - 15 years) (Sears et al. 2007, Wiener 2010). Many timber species, such as *Goupia glabra, Dypterix odorata* and *Tapirira guianensis*, are found in fallows of the study area. Management practices such as enrichment planting and thinning can enhance tree density and growth (Wiener 2010, Jakovac et al. 2014). Timber from fast-growing species is locally used for construction and could help supply local markets (Padoch et al. 2008).

Additionally, useful tree species could be favoured across the landscape in-between swiddens and fallows, as is already done for Brazil-nut trees (*Bertholletia excelsa*) in the study region (Paiva et al. 2011). Standing trees and saplings of this species are protected by farmers from weeding and burning, and fields are reshaped to avoid damaging them (Chapter 5). This practice results in an enriched landscape where crops and trees share the space, and could be extended to other species providing non-timber products such as *Carapa guianensis* and *Copaifera* spp. When fields have already surpassed the *tired-lands* threshold and regrowth is arrested, agroforestry is an alternative already applied by farmers to improve soil quality and at the same time provide nourishment and income to households.

Opportunities for sustainable development and conservation

Riverine communities have been historically ignored by public policies (Adams et al. 2009). Nowadays, however, several of these communities are comprised within protected areas that were established throughout the Brazilian Amazon. It is estimated that protected areas with resident communities cover 30.8 % of the Amazon region (RAISG 2012). Protected areas in Brazil embrace a few categories that have different regulations, such as indigenous lands, areas for strict nature preservation and categories that allow and give support to sustainable use of resources (e.g. RESEX and RDS; MMA, 2000). Protected areas are administered by the federal or state governments and NGOs (MMA 2000). These areas can play a key role in improving livelihoods in riverine Amazon, providing the means for a close interaction between traditional agriculture and nature conservation. In these areas, public policies that benefit local people have been more effectively implemented than in other remote areas of the Amazon. Moreover, in these areas local people have higher access to technical assistance, rural credits, and infrastructure, which can increase the possibilities for improving production and processing different products. The presence of these conditions under the goal of conserving nature and sustainably developing livelihoods, increases the chances of successfully implementing multifunctional landscapes. A few initiatives have been effective in enhancing social organization of riverine communities (as it is the case of the conservation unit RESEX Unini), improving market conditions for agricultural and forest products (e.g. RESEX Médio Juruá, RDS Rio Madeira) and fostering sustainable management of fishery (e.g. RDS Mamirauá and RDS Piagaçu-Purus). Protected areas could, therefore, support the adaptation of management practices to increase the sustainability of swidden cultivation systems and to foster multifunctional landscapes.

Supporting land use planning

Opposite to the general belief, swidden cultivation contributes little to deforestation at the Amazon region scale (< 12 % for the whole Amazon, Godar et al. 2014), and at the regional scale (< 20 %, Chapter 2; INPE 2013). Supporting swidden cultivation and traditional ways of living can help conserving cultural and natural resources in riverine Amazon (Padoch 2010, Parry et al. 2010b, Paiva et al. 2011). This thesis corroborates the idea that hinterlands provide opportunities for nature conservation, while landscapes around villages require closer attention on adapting management practices to avoid land degradation. I have shown that accessibility to land determines the boundaries of swidden cultivation landscapes, which are contained within a 2 km threshold from villages' housing area (Chapter 2). I also showed that areas closer to the housing area (< 1 km) are more intensively used (Chapter 2) and may be more prone to become degraded, needing closer attention for adapting management practices.

The results of this thesis expound linkages between land-use intensity, species composition of secondary forests and "ecosystem quality" (this Chapter), allowing for the identification of indicators that can help land-use planning. For describing land-use intensity in swidden cultivation systems, good indicators are the number of swidden-fallow cycles (Chapters 3, 4 and 5) and the fallow-period length (Silva-Forsberg and Fearnside 1997). Such information can be acquired through interviews with local residents or through remote sensing techniques, such as breakpoint detection applied to time-series (Chapter 2, Latifah 2015). Indicators of "ecosystem quality" identifiable through field assessments are the proportion of sprouting trees and the identity of the dominant species in secondary forests (Chapter 4). In wet secondary forests, high proportions of sprouting trees (> 50 %) indicates that the area has been intensively used and the plant community have reduced recovery capacity (Chapter 3). The dominance of early secondary forests by the tree species *Cecropia sciadophylla, Jacaranda copaia, Croton palanostigma, Cassia spruceana*, *Guatteria olivaceae* and *Vismia cayennensis* indicates increasing levels of land-use intensity and reduced recovery capacity and soil quality (Chapters 3 and 4). These species dominate secondary forests up to 20 or 30 years after abandonment and are wide-spread in the Amazon (Mesquita et al. 2001, Peña-Claros 2003, Barlow et al. 2007), being useful indicators in the Central Amazon region and beyond. The indicators of land-use intensity and "ecosystem quality" proposed here can be useful for land-use planning and to support decisions on assignment of areas for conservation, restoration or production purposes.

Challenges and opportunities of the farinha market

While in other regions permanent cultivation systems, pasturelands and cash crops are threatening traditional cultivation systems and staples (Padoch et al. 2007, van Vliet et al. 2013), in the Brazilian Amazon the strong cultural value of *farinha* is integrating smallholder farming to the market. This same market, however, also poses the challenge of producing *farinha* with a minimum environmental and cultural impact and guaranteeing smallholders' well-being.

Strong cultural value and the good match between a low nutrient-requiring crop and poor soils make *farinha* an encouraging product that connects riverine agriculture to the regional market. Cassava is a versatile crop that can be harvested year round allowing flexibility on the harvesting season (Elias et al. 2000, Fermont et al. 2008). Moreover, cassava can achieve reasonable yields without use of external inputs in swidden cultivation systems (Chapter 5), when the limits of ecosystem exploitation are respected. Independence from external inputs is desirable in remote areas where fertilizers reach prohibitive prices. Such characteristics have placed cassava at FAO's list of crops for poverty and food insecurity alleviation in agricultural frontiers (FAO and IFAD 2000). Moreover, after being processed, *farinha* can be stored for relatively long time, withstanding the long transportation hours that prevents perishable products from riverine areas to reach the urban centres (Salonen et al. 2012). Through rivers, *farinha* incorporates the traditional agriculture practiced quite distantly from the big centres, to the market, and may serve as an entry point for other local products, such as Brazil nut and fallow products, strengthening diversification.

Nevertheless, the current *farinha* market also imposes threats to local livelihoods by motivating unsustainable intensification and relying on a trading ruled by middlemen, which imposes price and product monopolies (Dias et al. 1998, Pereira et al. 2008). At the same time, public policies and rural extension institutions stimulate the standardization and homogenization of agricultural production, despising practices that promote diversification (Emperaire et al. 2012). Concerned about increasing *farinha* production, such institutions have been investing more on improving yield and homogenizing production rather than improving and organizing the supply chain (Emperaire et al. 2012). Therefore, to take advantage of this reality in riverine Amazon, the supply chain of *farinha* must be better organized to guarantee fair opportunities to farmers.

At the region of the middle-Amazonas river, a special type of *farinha* is produced, the so called *farinha ova* or *farinha do Uarini*. Processing of *farinha ova* is more laborious than the regular one, and is highly appreciated by consumers, being sold at higher prices at the market (although farmers not necessarily get better paid). Through the middlemen network, *farinha ova* flows downriver from the riverine communities to the regional market, Manaus, where it can be found at the supermarkets tagged as "*farinha do Uarini*", without further information on its actual origin. *Farinha ova* is a product from local farmers that should have its geographical indication of origin certified. Such certification could help improve the market chain (Emperaire et al. 2012). To make the *farinha* market a real and fair opportunity to smallholder farming, especially at riverine Amazon, it is essential to (i) promote coupled agriculture-environmental conservation policies, (ii) recognize and support the importance of knowledge on *farinha* production and beyond, allowing for a return of previous production systems that contained higher cassava diversity, and (iii) organize the supply chain in order to reduce intermediaries and guarantee fairness and security to smallholder farmers.

FINAL CONSIDERATIONS

By analysing a system where agricultural production is intrinsically dependent on the environment, this thesis brings insights on how management-environment interactions affect the resilience of a socio-ecological system. This thesis demonstrates the -many times overlooked- importance of management practices in determining the structure and species composition of secondary forests and the ecosystem services they provide. Based on these results, a conceptual framework is proposed to describe secondary succession in human-transformed landscapes (Figure 6.1). Additionally, it was found that agricultural intensification of swidden cultivation reduces crop yields and promotes the infestation by hard-to-weed species, inducing feedbacks that reinforce the negative effects of intensification on the environment and livelihoods. These findings combined with the farmers perceptions indicate that although farmers recognize thresholds for managing resilience, external forces may encourage overexploitation and push the system over this threshold. To enhance the resilience of swidden cultivation systems, it is required to improve the management of fallows and to broaden up the opportunities for adaptation. In the context of socio-ecological systems in riverine Amazon, resilience can be enhanced by broadening market opportunities beyond *farinha*, to include forest products that can be obtained within the swidden-fallow landscape, such as nuts, fruits and timber from fast-growing species. Thus, in human modified landscapes the proper management of secondary forests is key for promoting the integration of production and nature conservation.

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Summary

SUMMARY

In a world increasingly modified by humans, it is a challenge to guarantee the provision of resources to a growing human population while conserving biodiversity at the same time. To find an equilibrium between agricultural productivity and ecosystem integrity, it is important to understand how agricultural practices affect the resilience of socio-ecological systems. The traditional agricultural system in the tropics is swidden cultivation, also known as shifting cultivation. This system is based on the rotation of cropping fields and secondary-forest fallows. Secondary forests that develop during the fallow period provide ecosystem services that support the system, such as the fertilization of cropping fields, suppression of weeds and pests, and provision of useful species. However, the capacity of secondary forests to recover and provide such ecosystem services depends on the land-use history of the sites. The processes underlying the effects of land use remain unclear because concomitant effects of management, and soil and landscape configuration are rarely taken into account. Understanding how land use affects secondary forests recovery will help to improve management practices.

Socio-economic transformations in riverine Amazon in the last decades have taken place due to population migration and market integration. These transformations are inducing changes in the livelihood of riverine communities in the way swidden cultivation is done, leading to agricultural intensification. Agricultural intensification involves shortening the fallow periods and increasing the frequency of swidden-fallow cycles. The aim of this study was to evaluate how agricultural intensification affects the resilience of swidden cultivation in the region of the middle-Amazonas river. This region is one of the largest producers of cassava flour (*farinha* in Portuguese) in the Brazilian Amazon, which is the staple food of the region. By combining information from field surveys, farmers interviews and remote sensing, with farmers perception, I evaluated how the resilience of the socio-ecological system around cassava production is affected by agricultural intensification and related drivers.

In Chapter 2, we investigate how the processes of expansion and intensification of swidden cultivation took place in the last 30 years in riverine Amazon, and how land accessibility has determined land-use dynamics. We applied a novel remote sensing technique, the breakpoint detection algorithm, to Landsat time-series spanning from 1984 to 2013, to detect the frequency of swidden-fallow cycles and the length of the fallow period in agricultural fields. Our results showed that swidden expansion in old-growth forest has slowed down through time. Concomitantly, there was an increase in the frequency of swidden-fallow cycles and a decrease in the length of the fallow-period, from 9 to 5 years on average.

Expansion and intensification were associated with land accessibility, with fields closer to the housing area always being more intensively used, and with a threshold of walking distance from settlements (ca. 2 km) limiting field expansion and favouring intensification. As a consequence of the intensification process, the current landscape is predominantly covered by young secondary forests (≤ 10 years). This study showed that despite the apparent large availability of land in riverine areas, agricultural intensification is ongoing, leading to changes in land cover that may undermine the capacity of these landscapes to provide ecosystem services.

To evaluate the consequences of such intensification process on the productivity of the system, we evaluated how secondary forests and swiddens have changed along gradients of land-use intensity, in seven riverine villages. Given that the current fallow period in the region is short (≤ 5 years; Chapter 2), gradients of land-use intensity were represented by fields that had undergone different number of swidden-fallow cycles.

Along a gradient of land-use intensity, we sampled 38 secondary forests of the same age (5 years) to investigate the relative role of management intensity, soil properties and landscape configuration in determining the vegetation structure and species composition. In Chapter 3, we assessed the resilience of secondary forests as the recovery level of forest structure and species diversity that was achieved five years after abandonment. We used the recovery level achieved by secondary forests subjected to the lowest intensity of use as a reference, and interpreted a deviation from this reference level as a change in forest resilience. We found that with increasing number of cycles and weeding frequency, basal area and canopy height of the secondary forest sharply decreased, and that the percentage of sprouting and liana infestation on trees increased. With decreasing area covered by old-growth forest, species richness and diversity decreased. Soil conditions played a minor role. We concluded that land-use intensification reduces the resilience of secondary forests and ultimately may drive the system towards an arrested succession state that has less potential to support swidden cultivation systems.

In Chapter 4, we investigated whether such changes in vegetation structure were also related to species composition of successional plant communities. We investigated whether land use acts as a filter for species composition, and evaluated the relative roles of management practices, soil properties and landscape configuration. We found that management practices of cutting and burning filters out seed-dependent species and favoured sprouting species, and that soil quality determines the dominant species at higher land-use intensity levels. As a consequence of these local filters, species diversity decreases and early-communities become more similar to each other. We concluded that species composition of early-successional forests is strongly determined by land-use, and that filtering effects of management practices and soil quality at the onset of succession may invoke alternative successional pathways. We have identified indicator species that can be used to characterize the land use intensity to which secondary forests have been exposed.

In Chapter 5, we evaluate how the transformations associated with intensification are affecting livelihoods, by testing the hypothesis that agricultural intensification reduces swiddens productivity. Subsequently, we evaluated how this leads to changes in management practices. We observed that, as a result of market orientation, the diversity of crops and cassava landraces is lower than in other traditional systems. Moreover, only few tree species are being managed in swidden-fallow fields, due to the high focus on cassava as the main crop. Based on field surveys of 28 swiddens along gradients of land-use intensity, we observed that with increasing number of cycles, cassava yield decreases, weed cover increases and weed composition changes, with decreasing cover by trees and increasing cover by persistent graminoids. Changes in weed composition leads to increased demand for weeding labour. Consequently, farmers cultivate smaller swiddens, resulting in lower cassava production at the household level. Surprisingly, soil properties played a limited role, with number of swidden-fallow cycles overruling. We concluded that management practices have changed towards a higher focus on cassava as the main crop, reducing the inter- and intra-specific diversity of crops and the diversity of managed trees. The ongoing agricultural intensification, along with market orientation, is leading to lower swidden productivity without ensuing clear benefits for farmers.

The common result permeating the four research chapters of this thesis is the prevailing effect of number of cycles over landscape configuration and soil quality, on the productivity of swiddens and fallows. This dominant effect of number of cycles results from simultaneous changes in vegetation, soil conditions and farmers' management practices (Chapter 6). The decrease in the recovery rate of secondary forests is probably the result of decreased soil quality combined with the filtering effect of management practices that favours species that are strong-sproutings and are slow-growing. These species form secondary forests with limited potential to fertilize the next cropping cycle and to suppress weeds, resulting in higher demand for weeding, which in itself will further favour strong-sprouting species. Such interplay constitutes feedbacks that reinforce the adverse effects of intensification on the environment and for livelihoods. Farmers perceive this degradation process as the formation of *tired lands* (*terras cansadas* in Portuguese). From their perspective, a land would become *tired* after around four swidden-fallow cycles, and farmers would abandon the field to fallow for longer periods when land accessibility is not a limiting factor. Nevertheless, the combination of a low-nutrient-requiring crop, increasing *farinha* prices and shortage of accessible lands, is encouraging farmers to keep on cultivating also on *tired lands*, inducing further land degradation. Although farmers recognize thresholds for managing resilience, external forces seem to encourage overexploitation and push the system over such threshold.

The results of this thesis indicate that the resilience of swidden cultivation systems can be enhanced by breaking management-environment feedbacks through selective management of natural regeneration (including weeds). In the context of riverine Amazon, resilience can be enhanced by broadening market opportunities beyond *farinha*, to include forest products that can be harvested from the swidden-fallow landscape, such as nuts, fruits and timber from fast-growing species. Thus, in human modified landscapes the proper management of secondary forests is key for promoting the integration of production and nature conservation.

Acknowledgements

Doing a PhD is much more than writing a thesis. Doing a PhD is like being taken on a roller coaster of feelings with all kinds of professional and personal challenges, frustrations, achievements, stress and proudness. For me it was an intense and enjoyable journey thanks to the institutions, supervisors, colleagues, friends and family that supported me.

My journey started in 2011, when I came to the Netherlands accompanying my husband and looking for a PhD myself. I came to Wageningen with only a rough idea of a project (which ended up to be slightly different) and the willingness to do it. Fortunately I knocked at the right door and was welcomed by an amazing supervising team. I am deeply thankful to my supervisors from Wageningen University: Frans Bongers, Marielos Peña-Claros and Thom Kuyper, for welcoming that stranger and trusting her; and to my supervisor from Brazil, Rita Mesquita, for supporting me from the very beginning.

My (co-)supervisors are inspiring people and committed researchers with whom I have learned that doing science is a collaborative (and fun) work. Frans, your endless enthusiasm was always an injection of energy to carry on the work and to learn more. Thank you for pushing me forward when I needed and for always remembering us how delightful it is to learn new things every day. Also thanks to your wife, Yvonne, for the nice moments we shared in the Amazon and in the Netherlands. Marielos, you have been much more than a supervisor. You have supported me from the day I arrived in Wageningen, showing me the city around, organizing dinners, weekend trips and even helping furnish my house. Thank you so much for your friendship. You, Lourens and Franka were the family warming up our cold winters. Thank you Lourens for being a great step-supervisor and friend, with good advices, critical discussions, funny jokes and catching smiles. Thom, you have been very supportive during the development of my PhD project and was always very careful in every revision. With you I have learned a lot, not only about soils and fungi, but also about plants, ecology, writing, English, farmers, cassava and much more. Also thanks to your wife, Ali, for always being so kind and organizing many dinners with the cardumen. Rita, with you I got to know the Amazonian secondary forests. I am indebted with you for the many doors you have opened to me during my life in Manaus and for supporting me in all senses when I decided to go abroad for the PhD. Your commitment with nature conservation is inspiring. Thank you for your trust and friendship.

Along the PhD journey I have experienced different worlds. In the Amazon I have enjoyed the power of nature with its dynamic rivers, astonishing forests, startling tropical storms and spontaneous people. In the Netherlands I have seen the power of men to reinvent nature and to organize life. Learning the rationales and feelings of different cultures is a great opportunity provided by sandwich PhD programs. I am grateful to Wageningen University for admitting me in the PhD program and for providing an exceptional learning environment where I had access to an excellent library, very good courses, high quality research and to a diversity of subjects and cultures. I am grateful to the PE&RC and specifically to Claudius van der Vijver for the close and careful attention towards the PhDs. My home institution, the Instituto Nacional de Pesquisas da Amazônia – Inpa, is where I met great researchers fully committed with research, education, scientific divulgation and conservation of the Amazon. Thanks to the Coordenação de Capacitação from INPA, especially to Beatriz Ronchi Teles, for supporting me during the time I spent in Manaus and for providing the necessary conditions for my PhD research. Thanks to the Biological Dynamics of Forest Fragments Project (PDBFF), especially to the director José Luís Camargo and the staff members, who hosted me in a friendly atmosphere. The Soils Laboratory at INPA, especially to Jonas de Oliveira Filho, for helping me with the soil density analyses. I thank NUFFIC for funding this research through the Netherlands Fellowship Program-NFP (NFP 11/606; C&B-NFP-PhD.3246/11) and the National Institute of Environmental Services of the Amazon (Servamb-INCT) for the scholarship that covered part of my time in the field (Cnpq 381252/2013-2).

In Wageningen I had the opportunity to join an unique research group, which holds a friendly and motivating atmosphere, with nice people who like to discuss science, have coffee breaks and help each other. Many thanks to Frits Mohren, Pieter Zuidema, Lourens Poorter, Frank Sterck, Ute Sass-Klaassen, Ellen Wilderink, Danaë Rozendaal, Leo Goudzwaard, Jan den Ouden, Venceslas Goudiaby, Patrick Jansen, Merel Jansen, Gustavo Schwartz, Abeje Eshete, Tefera Mengistu, Motuma Tolera, Gabriel Muturi, Canisius Mungunga, Han van Tiep, Hooz Angela, Helen Esser, Paul Copini, Addisalem Bekele, Jilske van Swelm, Kwame Oduro, Kathelyn Paredes, Lucy Amissah, Marlene Soriano, Geovana Carreño-Rocabado and Lennart Suselbeek. Thanks to Joke Jansen for always knowing the answer to my questions, for her prompt assistance throughout these years, and of course for providing us cookies and cakes. Also thanks to the visiting researchers Flávia Mochel and Flávia Costa for the enjoyable moments shared in the Netherlands, and especially to Manuel Guariguata for contributing in the general discussion of this thesis. Special thanks to Mathieu Decuyper, Monique Weemstra, José Medina, Linar Akhmetzyanov, Jamir Afonso, Huicui Lu, Federico Alice, Edurne Marinez, Masha van der Sande, Madelon Lohbeck, Estela Quintero Vallejo, Peter Groenendijk, Mart Vlam and Carolina Levis, for the nice moments also outside the university. To my office mates Mart, Peter, Emiru and Estela, thanks for the nice working environment. Thanks to my compañera Estelita with whom I have shared the experiences of the PhD, the Netherlands, and of course of the International Club.

During these years I had learned a lot also with the master and internship students and with other colleagues who contributed to my thesis. I am grateful to Cristiano Alves (INPA), to Elisa de Veen (WUR), Andreas Peredo (WUR) and Latifah Siti (WUR) for helping me in the development of this research. I would also like to thank my colleague Loïc Dutrieux for the pleasant and fruitful collaboration we had.

In Manaus, at INPA, I had fruitful discussions that were key for the development of this research. At the Pioneiras research group I had the opportunity to collaborate with great people. Thanks to Bruce Williamson, Tony Vizcarra, Paulo Massoca, José Guedes and Gustavo Mahlé for the nice working environment and many discussions about secondary forests. Special thanks to Paulo Massoca for our friendly collaboration. Thanks to Paulo Maurício Graça and Claudia Vitel for guiding me on my first steps with remote sensing and GIS. I am also grateful to Charles Clement for the many discussions about *caboclos*, *farinha* and agriculture in the Amazon and for been so supportive since the very beginning and during this journey.

In Tefé I experienced the beauty of the Amazonian nature and people. In 2011 I arrived in Tefé ready to turn that research project into reality, but I had never been there before. It was thanks to the friendly people there that my field work was a success. Arriving at the airport of Tefé was the moment to meet Seu Carlinhos who many times drove me around and always managed to have piles of newspaper for my plant collections. Before and after going to the communities I had to stay a couple of days in the city, where I found the best field-base ever, a friend's house. Dear Leo and Tati thank you so much for hosting me so many times and for listening to my anxieties before going to the field and to my long stories on the way back. Also thank you so much for helping André and I when we had an accident and you were the best nurses one could have. I also thank Rafael, Rachel and Gabi, who hosted me a couple of times. My admiration for these friends that fight for the Amazon to be a better place for the local people and especially for the youth.

During field work I visited more than 40 villages before carrying out the more intensive surveys. These visits were only possible through the support I received from the Instituto de Desenvolvimento Agropecuário e Florestal Sustentável do Estado do Amazonas – IDAM of the municipalities of Tefé, Alvarães and Uarini, which allowed me to join in their field expeditions. Also thanks to the Instituto Mamirauá, especially to Bárbara Richers, Angela Steward, Fernanda Viana, Samis Brito and Jacson Silva for the many discussions and for allowing me to join you in an expedition to the Amanã Reserve. I am thankful to the staff of the Instituto Chico Mendes de Conservação da Natureza (ICMBIO), who are in charge of the FLONA Tefé: Astrogildo Moraes, Rafael Suertegaray Rossato and Gabriela Calixto, for kindly providing logistic support during all my field trips to the FLONA.

One of the best parts of this journey was the opportunity to meet wonderful people in the communities. Durante o desenvolvimento do meu trabalho nas cidades de Tefé, Alvarães e Uarini, eu sempre fui extremamente bem recebida. Muito obrigada a todos que me receberam em suas comunidades, que abriram a porta das suas casas, que me ofereceram um cafezinho, tucumã, açaí e farinha da melhor qualidade.

I am indebted with the farmers and their families who participated in this research and who were always extremely kind and helpful. Um agradecimento especial a todos os agricultores que se dispuseram a me mostrar suas roças e capoeiras e a responder tantas perguntas. Muito obrigada àqueles que participaram da pesquisa na Agrovila: Sr. Ilson, Dona Dora e família, Gil e família; Sr. Udson e Maria, Sr. Moacir, Sr. Manuel; Sr. Raimundo, Dona Cristina e família; Sr. Manuelito, seu filho Gelson e família; Sr. Francisco e Da Rosangela; Sr. Pedro; Sr. Chico Rocha; Sr. Zé Pretinho e Rosa; Sr. Jonas, Sr. Domingos e família; Na comunidade São Francisco: Sr. Gelson; Sr. Chico Magal; Sr. César e Dona Domar; Sr. Afonso e Dona Erimar; Luis e Márcia; Alan e Cláudia; Sr. Raimundo; Na comunidade Vila Sião: Sr. Leandro e família; Sr. Falcão, Dona Rosa e família; Sr. Odócio; Sr. Dedé; Sr. Humberto; Sr. Valdecy; Sr. José; Sr. Luis e família; Sr. Josimar; Sr. Enoque; Sr. Tomé e família; Sr. Joãozinho; Sr. Sheldo; Na comunidade Monte Carmelo: Sr. Egberto e Sr. Raimundo; Na comunidade Jauarituba: Sr. Zé Nilton; Sr. Zé Gonçalves; Sr. Zaqueu; Sr. Samuel e Sr. Gabriel; Na comunidade São Sebastião: Sr. Cosmo; Sr. João dos Santos; Sr. José; Sr. Militão; Sr. Armelindo; E na comunidade de Nogueira: Dona Idalina; Sr. Gustavo; Sr. Francelino; Sr. Edmilson; Sr. Jairo e Dona Marinete; Dona Maria Eugenia; Sr. Cisto. A colaboração de vocês e de suas famílias foi fundamental para o desenvolvimento desta pesquisa e por isso sou muito grata a todos vocês.

Special thanks to the families that kindly hosted me in their homes during the field work. Um agradecimento especial à famílias que me abrigaram com tanto carinho em suas casas durante o meu trabalho de campo. Agradeço de coração à família Falcão: Sr. Francisco Falcão, Dona Edna (Rosa), Reney, Franciele, Rênison, Radjane, Élida, e backspace, por acolher a mim e à Elisa na Vila Sião. Obrigada pelas tantas conversas e risadas na varanda e pelos domingos de descanso fazendo um peixe assado na praia. A ajuda e carinho de vocês fez o duro trabalho de campo ser muito mais prazeroso. Um agradecimento especial à Dona Rosa que me recebeu como uma amiga. Obrigada Armelindo e família por me receber em sua casa na Comunidade São Sebastião. Obrigada Jucelino e Sr. Raimundo e famílias por me receberem na Comunidade Bom Jesus. Obrigada Sr. Ilson, Dona Dora, Igor, Idson, Zé, Jane, Ismael e Anne, Gil, Val e os pequenos Gustavo, Giovani e Yara por me acolherem em sua casa na Agrovila e pelos deliciosos açaís. Dona Dora, encontrar aquelas deliciosas bananas fritas dentro da mochila do campo era o maior presente!

Thanks to the field assistants without whom this work would had been impossible to accomplish. Muito obrigada aos ajudantes de campo, sem os quais esse trabalho teria sido impossível: Sarney, Enrique, João dos Santos, Reney, Dona Rosa e Sr. Falcão. Um agradecimento especial ao Reney, que me acompanhou na maior parte do meu trabalho de campo. Obrigada Reney por toda a sua ajuda. Eu aprendi muito com você, e seu bom humor e disposição foram essenciais para sobrevivermos felizes aos carrapatos, vespas e carapanãs. Muito obrigada, foi um prazer trabalhar com vocês!

Surrounding the office and field works there are these people that help you survive the frustrations, celebrate the achievements and who can always find an excuse for having a party. Thank you all the friends from Manaus who make it such a lively and fun place to be, with lots of samba, suor e cerveja. Special thanks to Carlão, Ana Andrade and Natalia de Castro for being great friends and for making me laugh so much. Thanks to the friends that have transcended space and time and who are always there, wherever I am and whenever I arrive: Dani and Gabriel, Manô and Serginho (Bogs), Lucia Paçoquinha and Marco Gandhi, Simone Noni, Gabi Zuquim, Daniel Mindu and Ricardo Saci. Thank you all the friends in Wageningen who warmed up the harsh winters and the chilly summers with music, beers and smiles: Padraic, Renake, Alexandre, Ruthinha, Rafa, Julio, Gonzalo, Livia, Ben, Johannes, Madelon, Bas, Masha, Monique, Hans, Johan, Coen, Diana, Theo, Carol, Bernardo, Mathieu, Sara, Pelin, Johannes, Peter, Cathelijn, Rogier, Laura, Dorit, Peter and Isis. And thanks to the cardumen for assimilating me in the shoal: Clara, Tati, Paulo, Wellington, Angela, Camilo, André and Estela.

All the steps I took were only possible with the support from my family. I am grateful to my parents, brothers and sisters for their unconditional love and comprehension. My father Paulo and my mother Angela: you have always supported my decisions, even when they took me far away from you. Thank you for the opportunities you provided me, they allowed me to pursue my dreams. Thanks to my brothers Gustavo (and Simone) and Guilherme and to my sisters Natalia and Marilia for teaching me so much about relationships and for keeping our family united. Thanks to my nephews and nieces Vinícius, Julia and Paulinho, for bringing so much love to our lives. Obrigada à Tia Dorothy pelo seu apoio incondicional.

My other family was also very supportive, and I thank the Braga Junqueiras for understanding the reason why we had to be absent in so many family gatherings. Without your support we could never have done it! Thank you Lu, Tulio, João, Naty, Nic, Caio, Alice, Thiago, Dani, Carlota and Leléia for your support.

Finally, I thank André for our wonderful partnership and for making even the most elementary moment shine. Doing two PhDs at the same time was a challenge to our relationship, but we took it as a team work and we evolved together in every sense of life. Dé, to be at your side is to feel at home wherever we are. Thank you for being on my side.

I am confident that the PhD wouldn’t have been so rewarding without these great people around me.

Thank you all!

Hartelijk bedankt!

Muito obrigada!

SHORT BIOGRAPHY

Catarina C. Jakovac was born on the 12th of May 1981 in São Paulo (Brazil). She studied elementary school at the Colégio Notre Dame and high school at Colégio Etapa. From 2000 to 2003 she studied Biological Sciences at the Universidade de São Paulo – USP.

During her bachelor she did an internship on marine biology at the Oceanographic Institute of USP, where she completed her bachelor thesis on the ecology of diatoms in the estuary of Cananéia, São Paulo, Brazil. After completing her studies she moved to Piracicaba to work at the Laboratory of Forest Ecology and Restoration (LERF in Portuguese) at ESALQ/USP. During 2004 she worked on the monitoring of native and restored forests in the Atlantic Forest of São Paulo State. By the end of that same year she started her masters on Plant Biology at the Universidade de Campinas (UNICAMP) under the supervision of Dr. Ricardo Ribeiro Rodrigues, to evaluate the use of forest topsoil to restore mining landfills. In 2006 she was selected to participate in the field course on Ecology of the Amazon Forest – EFA, promoted by the Instituto Nacional de Pesquisas da Amazônia-INPA. It was the first time she went to the Amazon and when she got most excited about doing science.

In 2007 she defended her master thesis and moved to Manaus, Amazonas. In Manaus she joined the Biological Dynamics of Forest Fragment Project (PDBFF in Portuguese) as a fellow researcher at the Projeto Pioneiras led by Dr. Rita Mesquita, to study the effects of land use on secondary succession and to evaluate alternatives for restoring and managing secondary forests. Catarina is currently still collaborating with the Projeto Pioneiras.

Parallel to her research activities, in 2010 she worked at the Museu da Amazônia – MUSA coordinating a rural extension project to develop organic production at the peri-urban zone of Manaus. She brought courses on agroecological production and social organization to farmers, which allowed them to establish an organic horticulture and to sell their produce in the local organic market after one year. The project is still running by MUSA but Catarina decided to do her PhD in the Netherlands.

In April 2011 she started the PhD at Wageningen University in collaboration with the Instituto Nacional de Pesquisas da Amazônia-INPA. During the PhD she attended several international meetings and had the opportunity to present and discuss her research with different researchers, which contributed to this thesis.

Catarina is interested in studying the human impact on forests and landscapes to improve land-use planning and restoration actions. She wants to continue working on the topics of land-use change, secondary succession and restoration ecology in tropical landscapes and is especially interested in applied research and interdisciplinary studies.

LIST OF PUBLICATIONS

Published/accepted articles

Mesquita, R.C.G., P. Massoca, C.C. Jakovac, T.V. Bentos, G.B. Williamson. Amazon rainforest succession: Stochasticity or land-use legacy? *Bioscience*, in press. 2015

Jakovac, C.C., M. Peña-Claros, T.W. Kuyper, F. Bongers. Loss of secondary-forest resilience by land-use intensification in the Amazon. *Journal of Ecology* 103: 67-77. 2015

Jakovac, A.C.C., T.V. Bentos, R.C.G. Mesquita, G.B. Williamson. Age and light effects on seedling growth in two alternative secondary successions in central Amazonia. *Plant Ecology and Diversity* 7: 349-358. 2014.

Massoca, P.E.S., A.C.C. Jakovac, T.V. Bentos, G.B. Williamson, R.C.G. Mesquita. Dinâmica e trajetórias da sucessão secundária na Amazônia Central. *Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais*, 7: 235-250. 2012.

Souza, S.M., A.B. Junqueira, A.C.C. Jakovac, P.A. Assunção, J.A. Correia. Feeding behavior and ophiophagous habits of two poorly known Amazonian coral snakes, *Micrurus albicinctus* Amaral 1926 and *Micrurus paraensis* Cunha and Nascimento 1973 (Squamata, Elapidae). *Herpetology Notes*, 4: 369. 2011.

Submitted articles

Jakovac, C.C., F. Bongers, T.W. Kuyper, R.C.G. Mesquita, M. Peña-Claros. Land use as a filter for species composition in Amazonian secondary forests.

Jakovac, C.C., S.H. Latifah, L.P. Dutrieux, M. Peña-Claros, F. Bongers. Spatial and temporal dynamics of swidden cultivation in riverine Amazonia: expansion and intensification.

Jakovac, C.C., M. Peña-Claros, R.C.G. Mesquita, F. Bongers, T.W. Kuyper. Swiddens under transition: consequences of agricultural intensification in the Amazon.

Dutrieux, L., C.C. Jakovac, S.H. Latifah, L. Kooistra. Reconstructing land use history from Landsat time-series: Case study of a swidden agriculture system in Brazil.

Poorter, L., F. Bongers, M. Aide, A.M.A. Zambrano, P. Balvanera, J. Becknell, V. Boukili, E. Broadbent, R. Chazdon, D. Craven, J.S.De Almeida-Cortez, G.A.L. Cabral, B. De Jong, J. Denslow, D. Dent, S.J. Dewalt, J.M. Dupuy, S.M. Durán, M.M. Espírito-Santo, M.C. Fandino, J. Hall, J.L.H. Stefanoni, C.C. Jakovac, A.B. Junqueira, D. Kennard, S. Letcher, M. Lohbeck, E. Marín-Spiotta, M. Martínez-Ramos, P. Massoca, J.A. Meave, R. Mesquita, F. Mora, R. Muñoz, B. Muscarella, Y.R.F. Nunes, S. Ochoa-Gaona, E.O. Belmonte, M. Peña-Claros, E.A. Pérez-García, D. Piotto, J.S. Powers, J. Rodríguez-Velazquez, I.E. Romero-

Pérez, J. Ruíz, L. Sanaphre, A. Sanchez-Azofeifa, N. Swenson, M. Toledo, M. Uriarte, M. Van Breugel, H. Van Der Wal, M.D.M. Veloso, T.V. Bentos, G.B. Williamson, D.M.A. Rozendaal. Biomass resilience of tropical secondary forests.

Rozendaal, D.M.A., R.L. Chazdon, F. Arreola-Villa, P. Balvanera, T.V. Bentos, J.M. Dupuy, J.L. Hernandez-Stefanoni, C. C. Jakovac, E.E. Lebrija-Trejos, M. Lohbeck, M. Martinez-Ramos, P.E.S. Massoca, J.A. Meave, R.C.G. Mesquita, F. Mora, E.A. Perez-Garcia, I.E. Romero-Perez, M. Van Breugel, G.B. Williamson, F. Bongers. Contrasting aboveground biomass dynamics during secondary succession in Neotropical dry and wet forests.

PE&RC TRAINING AND EDUCATION STATEMENT

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- Consequences of agricultural intensification of swidden cultivation

Writing of project proposal (3 ECTS)

- Consequences of traditional agriculture intensification for secondary forest resilience and ecosystem services in Brazilian central Amazonia

Post-graduate courses (9.2 ECTS)

- Generalized linear models; WUR (2011)
- Mixed linear models; WUR (2011)
- Linear models; WUR (2011)
- Multivariate analysis; WUR (2013)
- Introduction to R; INPA, Brazil (2013)
- Alternet summer school; Multi-institutional, include Alterra (2013)
- Soils spring school: world soils and their assessment; ISRIC (2014)

Deficiency, refresh, brush-up courses (5.7 ECTS)

- Advance forest ecology and management (2011)
- Basic statistics; WUR (2011)
- Introduction to GIS for conservation; IPÊ Institute, Brazil (2013)

Competence strengthening / skills courses (3 ECTS)

- Competence assessment (2011)
- Techniques for writing and presenting a scientific paper (2014)
- Time and project management (2014)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.2 ECTS)

- PE&RC Weekend (2011)
- NERN Meeting (2011)

Discussion groups / local seminars / other scientific meetings (4.5 ECTS)

- Ecology theory and application (2014, 2015)
- FEM Journal club (2013, 2014, 2015)

International symposia, workshops and conferences (8.5 ECTS)

- Meeting of the Association for Tropical Biology and Conservation-ATBC (2012, 2014)
- Intecol, annual meeting of the British Ecological Society (2013)
- GTÖ, Annual meeting of the Society for Tropical Ecology (2015)

Lecturing / supervision of practical's / tutorials (1.2 ECTS)

- Ecological methods (2015)

Supervision of MSc students (9 ECTS)

- Land use effects on understory vegetation during early succession in Central Amazon Brazil; Elisa de Veen (2012)
- Forest recovery from slash and burn agriculture from remote sensing time-series; Latifah Siti (2015)
- Drivers of liana community structure in Central Amazon: the impact of environment and land use history; Andrés Peredo (2014)

The research described in this thesis is in accordance with the Brazilian Nacional Committee in Ethics in Research (CONEP) and was approved by the Ethics Committee of the National Institute of Amazonian Research (Comissão de Ética em Pesquisa do Instituto Nacional de Pesquisas da Amazônia, CEP/INPA; Br) under the project number 20361713.7.0000.0006. All interviewed farmers provided their written consent, which had been previously approved by CONEP and CEP/INPA. Surveys inside the protected area FLONA Tefé were authorized by ICMBIO (SISBIO 34294-2).

This research was financially supported by Wageningen University (Sandwich grant 11/00220; NL), NUFFIC (NFP 3246/11; NL), and The National Institute for Environmental Services of the Amazon (Cnpq/Servamb 381252/2013-2; Br).

Financial support from Wageningen University for printing this thesis is gratefully acknowledged.

Photography by Catarina C. Jakovac

Cover design by GVO Drukkers & Vormgevers B.V.| Ponson & Looijen, Ede, The Netherlands

Printed by GVO Drukkers & Vormgevers B.V.| Ponson & Looijen, Ede, The Netherlands