Resilience of Amazonian forests

The roles of fire, flooding and climate

Bernardo Monteiro Flores

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Chapter 1

General Introduction

Bernardo M. Flores

With global warming, extreme climatic events are becoming more common (IPCC 2014), testing the capacity of natural systems to persist. A fraction of these systems are known for having alternative basins of attraction, or alternative stable states, implying that gradual changes in an external forcing such as climate may push the system from one basin to the other (Scheffer et al. 2001). For instance, moist tropical lands can be found in either the forest or savanna state. Shallow lakes can be in a clear or turbid state, and the shift between both states can happen suddenly (Scheffer et al. 2001). These ecosystems are especially vulnerable, because unexpected ecological transitions may alter biome and species distribution across landscapes. Such drastic changes have implications for habitat availability (Hoekstra et al. 2005), threatening biodiversity and ecosystem services (Cardinale et al. 2012). Therefore, assessing ecological resilience is of broad scientific and societal interests. Understanding the drivers of ecological transitions may allow societies to manage ecosystem resilience, ensure conservation and promote restoration when necessary (Scheffer et al. 2015a). This approach has been explored in both terrestrial (Holmgren et al. 2006; Sitters et al. 2012) and aquatic systems (Hughes et al. 2007; Kosten et al. 2012).

Holling (1973) coined the term ‘ecological resilience’ to characterize a system's capacity to remain in the same state in the face of perturbations. In his view, if the basin of attraction that corresponds to one state becomes smaller, the system's resilience in that state is lost, implying that a stochastic event is more likely to push the system to the alternative state . Most studies have addressed the ecological resilience of ecosystems using conceptual and modelling approaches (Walker et al. 1981; Kefi et al. 2007; Anthony et al. 2011; Dakos et al. 2011; van Nes et al. 2014; Magnuszewski et al. 2015; van de Leemput et al. 2016). Some attempts have inferred resilience through analysis of remote sensing data in different ecosystems (Hirota et al. 2011; Staver et al. 2011; Xu et al. 2015; Staal et al. 2016). Few assessed the resilience in nature with all of its complexity (Acacio et al. 2007; Graham et al. 2015; Jakovac et al. 2015). In my thesis, I studied the mechanisms that shape Amazonian forest resilience. Combining satellite data, field surveys and experiments, I assessed whether Amazonian forests may shift into a savanna state under recurrent fire conditions.

Resilience theory applied to tropical forest systems

There are several ways to measure the ecological resilience of ecosystems. One is the analysis of the frequency distribution of massive data that may reveal the potential existence of alternative stable states from multimodality (Scheffer et al. 2015b). The analysis of massive spatial data on tropical tree cover revealed that alternative states in the vegetation may exist in the same range of rainfall conditions (Hirota et al. 2011; Staver et al. 2011). In the wet tropics, two modes in the frequency distribution of tree cover suggest that forest and savanna are alternative attractors, and imply that stochastic events may push the system from one state to the other (Scheffer et al. 2001). The existence of alternative attractors in tropical vegetation can in part be explained by the abrupt increase in fire probability when tree cover drops below 50%, (Archibald et al. 2009). This positive feedback mechanism stabilizes forests and savannas, maintaining sharp vegetation boundaries in tropical landscapes (Dantas et al. 2016). As a result of this long-term vegetation dynamics, the distribution of tree cover may reflect the average time that different parts of the ecosystem spend in each basin of attraction (Hirota et al. 2011).

Ecological resilience varies as a function of external stressing conditions, such as drought or grazing (Walker et al. 1981). When stressing conditions increase upon ecological systems, their recovery from perturbations becomes slower indicating loss of resilience (van Nes and Scheffer 2007), and announcing that the system approaches a tipping point (Scheffer et al. 2009). Analyses of tropical tree cover distribution reveals that below 1000 mm of annual rainfall forest tree cover values are strikingly rare, suggesting this may be a tipping point for forest collapse (Hirota et al. 2011; Staver et al. 2011). Therefore, as rainfall conditions lower towards this threshold, forest recovery is expected to slow down, increasing the chance that a small perturbation may push the system to the savanna basin of attraction. Evidence for the neotropics that the recovery rate of forest biomass after human disturbance reduces sharply below ~1500 mm of annual rainfall, supports this idea (Poorter et al. 2016). A recent study showed that when tropical systems approach this tipping point in rainfall conditions, savannas already seem to be relatively more stable than forests and potentially more likely to expand (Staal et al. 2016). There is limited field evidence on tropical forest resilience relative to external and also environmental conditions (van Nes et al. 2014). Jakovac et al. (2014), have shown for instance that forest recovery slows down after repeated cycles of shifting cultivation in the Amazon forest. Although forest recovery in tropical systems seem to slow down with drought and repeated disturbances, evidence of forest savannization is rare (Cavelier et al. 1998), suggesting a high capacity to persist in the forest state.

Evidence of past shifts in tropical vegetation

If present day spatial distribution of tropical tree cover is the result of long-term shifts between forest and savanna (Hirota et al. 2011; Staver et al. 2011), the analysis of historical vegetation dynamics should reflect this pattern (Willis and Birks 2006). In Amazonian ecotones, shifts between forest and savanna occurred several times during the past thousands of years (Mayle and Power 2008). Forests expanded during periods of wetter climate, whereas savannas expanded in times of drought and when human-ignited fires were more common. The origin of large savannas at the south and north edges of the Amazon, the Llanos de Moxos (Mayle et al. 2007), and the Gran Savanna (Montoya et al. 2011), are in part attributed to indigenous land management with fire. Other savanna islands across the Amazon forest were found to be strikingly confined to ancient river channels (Rossetti et al. 2012). The authors attribute this pattern to recent deactivation of alluvial sedimentary dynamics, allowing the development of open vegetation. An alternative explanation for the persistence of these savanna islands, however, may be the combination of seasonal flooding with frequent fires (Prance 1996; Mayle et al. 2007).

The study of past vegetation dynamics in relation to climate, fire and environmental factors, such as flooding, is important for allowing a mechanistic understanding of what drives shifts between forest and savanna. Detailed analysis of present-day tree cover distribution provides another insightful perspective (Hirota et al. 2011; Staver et al. 2011). This is especially important as climate change is expected to increase the frequency of drought episodes in tropical regions (Cai et al. 2014; Lau and Kim 2015). Global climate models predict that savannas will expand at the borders of the Amazon forest in the near future as a response to climate change (Cox et al. 2004; Malhi et al. 2009). Such expectation highlights the need for detailed assessment of what happens to tropical forest resilience that results in the transition to savanna.

Satellite versus field perspective of forest and savanna

Satellite tree cover data (Hansen et al. 2003) is commonly used to assess forest and savanna distribution, and their relative resilience as a function of external conditions (Archibald et al. 2009; Hirota et al. 2011; Staver et al. 2011; Staal et al. 2016). However, the real complexity that defines forest and savanna in nature involves the composition of species and functional traits, which are not measurable from satellite (Ratnam et al. 2011). Satellite data allow assessing a limited number of variables that describe the vegetation, and the environment. However, they also allow assessing universal patterns, which would never be possible with field data. The interpretation of a mere perspective of complex reality requires certain assumptions. In **Chapter 2**, I use the percent tree cover data at 250 m spatial resolution (DiMiceli et al. 2011), to assess the resilience of Amazonian floodplain and upland forests. For this I assume that upland and floodplain ecosystems are spatially homogeneous, and that positive feedback mechanisms are necessary to stabilize the vegetation in each basin of attraction (Fig. 1.1) (Murphy and Bowman 2012).

Another limitation of tree cover data is that it fails to distinguish forest from closed canopy savanna (Ratnam et al. 2011), and savanna from degraded forest (Veldman and Putz 2011). The main reason is that MODIS tree cover considers as tree all crowns above 5 m in height (DiMiceli et al. 2011). Therefore, it does not detect the contrasting canopy heights of forest and savanna tree communities (Xu et al. 2016). Tree cover data provides structural information on canopy cover, but not details that really define forest and savanna such as plant adaptations to fire (Ratnam et al. 2011). For this reason, the ideal approach to assess the mechanisms for such bistability is by combining the analyses of satellite tree cover with fire data, and field validation.

The role of fire on forest savannization

Both palaeoecological and satellite data support the notion that fire has an important role in the bistability of tropical vegetation (Mayle and Power 2008; Archibald et al. 2009; Staver et al. 2011). Nonetheless, this is still under intense scientific debate (Staal and Flores 2015). Some defend that the distribution of forest and savanna is determined by climatic-edaphic envelopes (Quesada et al. 2012; Rosseti et al. 2012; Veenendaal et al. 2015). Others explore the role of a positive feedback mechanism between plants and fire (Cochrane et al. 1999; Hoffmann et al. 2012; Murphy and Bowman 2012; Dantas et al. 2016). In savannas, herbaceous vegetation co-exists with adult savanna trees, spreading fires that kill forest trees that attempt to recruit (Bond and Midgley 1995; Sankaran et al. 2004; Silva et al. 2013). This positive feedback traps the system in a low tree cover state (Grady and Hoffmann 2012). However, when fire is excluded from the system, forest trees are able to recruit (Moreira 2000; Higgins et al. 2007; Pellegrini et al. 2015), promoting canopy closure and suppressing fire (Murphy and Bowman 2012; Silva et al. 2013). Most studies consider that the availability of resources across the landscape, such as soil fertility, determines the rate of forest growth and the chance that a system can be trapped by fire in a savanna state (Hoffmann et al. 2012; Murphy and Bowman 2012; Dantas et al. 2016). A third hypothesis, however, is that soil can change due to local interactions with fire and vegetation, contributing to stabilize forests and savannas (Fig. 1.1), or to accelerate transition between both states (Jackson 1968; Wood and Bowman 2012; Silva et al. 2013; Pellegrini et al. 2014; Franco et al. 2014; Paiva et al. 2015).

When fires percolate in rainforests, the vegetation can be impacted in many ways. In the Amazon, forest fires can alter tree composition by selecting pioneer trees (Barlow and Peres 2008), trees with higher tolerance to fire (Veldman and Putz 2011), or with resprouting ability (Jakovac et al. 2015). Nonetheless, the persistence of forest tree species allows the system to recover canopy closure in a short time (Mesquita et al. 2001; Jakovac et al. 2015; Devisscher et al. 2016). Due to the apparently high resilience of Amazonian forests (Poorter et al. 2016), the mechanisms that could drive forest savannization remain uncertain. For instance, under recurrent fire, the invasion of herbaceous plants is limited to the forest edge (Silverio et al. 2013; Brando et al. 2014). Disturbed forests are mostly dominated by few non-native herbaceous species, contrasting with the diverse herbaceous layer of true savannas (Veldman and Putz 2011). In fact, rare studies across the tropics have demonstrated forest savannization. In South America, centuries of land-use with fire and cattle allowed soils of moist tropical forests to erode intensely, favouring the colonization of savanna trees (Cavelier et al. 1998). This suggests that chronic perturbations that allow resource conditions to degrade (Shakesby and Doerr 2006) may lead to savannization, if savanna trees are able to disperse into disturbed sites.

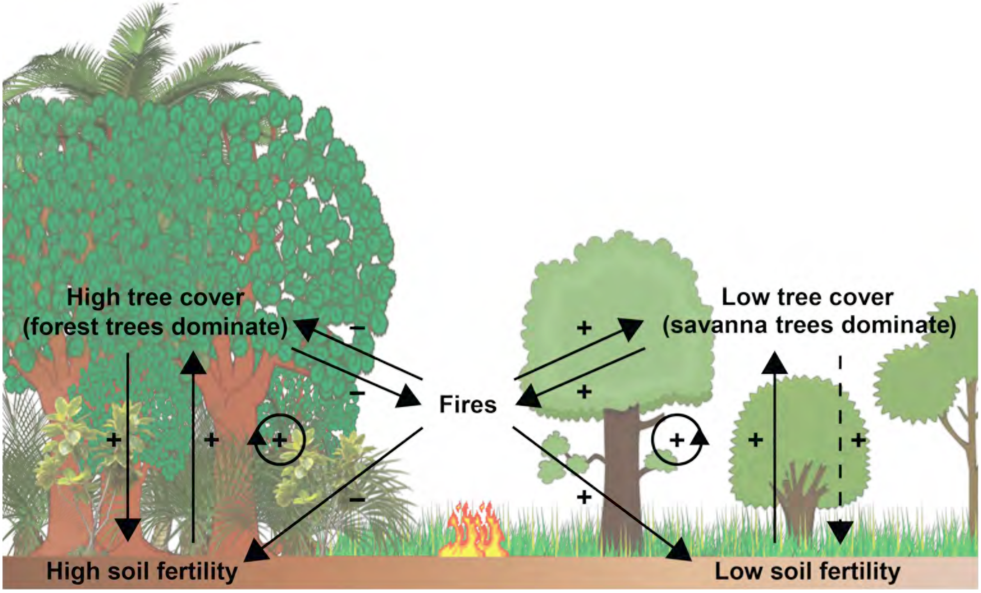

Figure 1.1. Mechanisms maintaining tropical bistability (adapted from Staal and Flores 2015). In this thesis I assessed how fire can alter such mechanisms and trigger a forest-savanna transition.

Ecology of Amazonian floodplain and upland ecosystems

One seventh of the Amazon basin is formed by seasonally flooded ecosystems (Hess et al. 2015). The larger area is covered by non-floodable *terra firme* ecosystems (86%), which I refer to as uplands. Floodplains differ from uplands in many ways, as life has to adapt to an annual flood pulse, altering between the terrestrial and aquatic phases (Junk et al. 1989). The Amazonian rainfall season is followed by a flood wave that moves down the rivers spreading the onset of the aquatic phase (Richey et al. 1989). Due to the predictability of such disturbance, life can flourish with special adaptations (Parolin et al. 2004; Keddy et al. 2009). For instance, 3.500 species of fish are estimated to live in the Amazon basin, of which 50% are associated with floodplains (Junk et al. 2007).

The number of tree species that occur in Amazonian floodplain habitats is probably close to 1500, as only in white and black water floodplains 1000 and 600 species are estimated to occur, respectively (Wittmann et al. 2006; Junk et al. 2015). Hence, of the 16000 tree species estimated to exist in the entire Amazon (ter Steege et al. 2013), approximately 10% occur in the floodplains. Moreover, of the 227 hyper dominant Amazonian trees, one fourth is specialist to seasonally inundated habitats (ter Steege et al. 2013). Hence, floodplain trees are also important for broad-scale ecosystem functions such as carbon cycling (Fauset et al. 2015). Despite inundation, adjacent floodplains and uplands share more than 30% of tree species (Terborgh and Andresen 1998; Wittmann et al. 2006), revealing connectivity between both ecosystems.

Floodplain forests across the Amazon have an average aboveground live biomass of 160 tons per ha^{-1} (±100 of SD) (Saatchi et al. 2007). The variation is likely associated with distinct habitats and water types (Junk et al. 2011). Rivers that carry white water originate in the Andes, from where they transport huge loads of sediment and nutrients. Their floodplains are highly productive ecosystems (Junk et al. 2011), and represent half of Amazonian floodplains (Melack and Hess 2010). In contrast, black and clear water rivers are poor in sediments and nutrients, and have floodplains with low fertility (Junk et al. 2011). The acid and nutrient-poor black water that flows in countless streams and tributaries born in the forest has major influence on half of Amazonian floodplains (Melack and Hess 2010). Due to these differences in fertility, tree growth rates contrast sharply between white and black water floodplains (Schongart et al. 2005). Another difference is related to the fine root system. Black water forests have a root mat to avoid nutrient leaching (Stark and Jordan 1978; dos Santos and Nelson 2013), whereas in white water floodplains root mats are typically absent (Meyer et al. 2010). In addition, Amazonian floodplains also include peatlands (Lahteenoja et al. 2009, 2013), swamps, palm forests, white-sand forests, and extensive islands of savanna (Prance 1996; Junk et al. 2011).

Upland forests have an average aboveground live biomass of 250 tons per ha^{-1} (Saatchi et al. 2007), which varies across habitats (100 tons per ha^{-1} of SD). Basin-wide environmental gradients explain most of the variation in forest structure and dynamics (Quesada et al. 2012), as well as in tree composition and function (ter Steege et al. 2006). For instance, total phosphorous and soil physical properties determine forest dynamics across the basin (Quesada et al. 2012). Dry season length and soil fertility are good predictors of tree functional composition (ter Steege et al. 2006). The western Amazon is the region that receives more rain throughout the year, and has more fertile soils due to a major geological process. As a result of the Andean uplift, the nature of South America changed drastically ~12 Ma ago (Hoorn et al. 2010). Around 7 Ma ago the Amazon river was formed and began to supply nutrients from the Andes to the Amazon basin (Hoorn et al. 2010). In the same time, massive wetlands in the western Amazon started retreating, allowing the expansion of new upland habitats. In contrast, upland forests of the Guiana Shield region have the poorest soils of the Amazon basin, and concentrate tree species with special adaptations such as large seeds (ter Steege et al. 2006).

In the central Amazon region, field measurements show that the impact of a fire event is much higher on floodplain than on surrounding upland forests (Resende et al. 2014). Analysis of post-fire recovery of the forest structure from satellite suggests that floodplains are less resilient than uplands (Flores et al. 2014). However, broad-scale analyses are necessary to test if this pattern is consistent across the Amazon basin, and field assessments are necessary to unravel the mechanisms. One reason could be that seasonal flooding reduces forest recovery rate by limiting tree growth (Schongart et al. 2002). In blackwater floodplains, forest regrowth after fire may also be slowed down by nutrient limitation due to intense leaching (Shakesby and Doerr 2006).

Thesis outline

The central hypothesis of my PhD thesis is that floodplain forests of the Amazon are less resilient to fire perturbation than surrounding upland forests, and therefore more likely to shift into a savanna state. To address this hypothesis, I develop different approaches, combining satellite data, field assessments and field experiments.

Chapter 1 provides some background on ecological resilience, tropical forest-savanna transitions, and the ecology of floodplain and upland ecosystems of the Amazon.

In **Chapter 2**, I analyze broad-scale patterns of Amazonian forest resilience using satellite tree cover data, and contrasting floodplain and upland ecosystems. I also compare the post-fire rates of forest recovery and soil degradation between both ecosystem types, using satellite tree cover and field data on tree basal area and soil properties.

In **Chapter 3**, using field data I show the patterns of natural post-fire recovery of blackwater floodplain forests after one and two fire events. I measured forest structure, species richness, tree seed banks, root mat, and herbaceous cover, to assess changes in forest recovery rate.

In **Chapter 4**, I reveal what happens to the soil and tree composition of floodplain forests after fire. I use space-for-time to produce a chronosequence and test the hypothesis that after fire, soils degrade due to leaching, and savanna tree species become dominant.

In **Chapter 5**, I test the hypotheses that post-fire recovery is delayed by recruitment limitations. I combine inventories of tree seed availability in floodplain burnt sites, with an experimental assessment of environmental filters for planted tree seedlings.

A synthesis bridging the findings of this thesis with previous knowledge is developed in **Chapter 6**. From the perspective of Amazonian seasonally flooded ecosystems, I attempt to broaden the understanding of tropical forest-savanna transition.

Chapter 2

Resilience of Amazonian forests

Bernardo M. Flores, Milena Holmgren, Chi Xu, Egbert H. van Nes, Catarina C. Jakovac, Rita C. G. Mesquita, Marten Scheffer

Abstract

Amazonian rainforests are among the most resilient in the world. Although these forests may seem quite homogeneous, 14% is seasonally inundated. Here we analyze tree cover distribution for the whole Amazon system to reveal that under comparable precipitation regimes, savannas are more common on these floodable areas. This suggests that compared to upland forests, floodplain forests are less resilient to shifting into a savanna state. Combining satellite data and field measurements we show that the apparent low resilience of floodplain forests may be explained by a high sensitivity to fire. The comparison of fire impact on both ecosystems reveals that in floodable forests, tree cover is reduced more severely, forest recovery is slower, and soil degradation is faster compared to upland forests. Recent drought events have shown that fires can percolate through massive stretches of forest. Our results imply that floodable Amazonia may be a sensitive starting point for forest collapse from such wildfires.

The Amazon forest has recently been shown as a resilient system with high capacity to recover its biomass after perturbations (Poorter et al. 2016). A striking natural variation in the character of forests in the wet Amazonian system, however, is related to seasonal inundations, yet the role of inundation on forest resilience had never been assessed over a broad scale. About one-seventh of Amazonian forests are inundated a substantial part of the year (Hess et al. 2015), causing these ecosystems to differ in many ways from the dominant upland *terra-firme* forests (see Methods).

Here we ask how seasonal inundation plays out when it comes to resilience against shifting into a fire-dominated savanna state. We use three approaches to contrast floodplain and upland forests (Fig. 2.1 a, b). First, we compare the probability density of satellite derived tree cover as an indicator of relative forest and savanna resilience (Hirota et al. 2011; Scheffer et al. 2015b) using 2001 MODIS vegetation continuous field (VCF) data at 250 m resolution for the whole Amazon basin (Methods). Second, we systematically compare the short- and long-term effects of a series of forest fires that occurred in both systems during the severe droughts of 1997 and 2005. For this we use 30m-resolution Landsat images spread across most of the rainfall gradient (Appendix 2.1) to identify over 250 burnt sites (Appendix 2.2), and annual MODIS VCF data to analyze recovery dynamics (Methods). To validate the remote sensing analyzes of tree cover recovery, we use field data from the central Amazon region (Appendix 2.1) to compare the rates of tree basal area recovery after fire in both systems.

Third, using the same field data, we compare rates of soil leaching after the first fire, when mature forests were converted into open vegetation. For this we analyze changes in soil texture and fertility using space-for-time to produce chronosequences of up to 70 years after the first fire.

The rationale behind studying the probability density of tree cover is that, under otherwise homogeneous conditions (van Nes et al. 2014; Scheffer et al. 2003) probability densities of states may reveal alternative attractors and their relative resilience (Hirota et al. 2011; Scheffer et al. 2015b). Applied to spatial data, this approach assumes that the states of different grid-cells reflect snapshots of the dynamics of several individual systems (Scheffer et al. 2003; Livina et al. 2010; Hirota et al. 2011; van Nes et al. 2014; Scheffer et al. 2015b). In Amazonian uplands, the probability density distribution of tree cover has a single mode around 84 % reflecting dense forest, with sparse tree cover being rare (Fig. 2.1 d, Appendix 2.3). In contrast, floodable areas have an additional mode around 34 % tree cover, reflecting the presence of a savanna-like state (Fig. 2.1 c, Appendix 2.3). This difference between uplands and floodplains occurs especially in the relatively drier regions where mean annual precipitation falls below 1,500 mm (Fig. 2.1 e, f). Assuming the probability densities (Fig. 2.1 b, c) to reflect underlying long-term dynamics of a stochastically perturbed system, the ratio of the number of observations falling in the two modes indicates their relative resilience (Hirota et al. 2011; Scheffer et al. 2015b). Taking 60% tree cover as the cut-off point for forests and savannas, previously shown a rare tree cover across the tropics (Hirota et al. 2011), it is clear that relative forest resilience is markedly lower in the floodplains than in uplands (ratios of 66/34 versus 93/7 in Fig. 2.1 b, c; Appendix 2.4). A closer look reveals that the difference is particularly pronounced in drier parts (Appendix 2.5). A marked savanna mode occurs below 1,500 mm of mean annual precipitation on the floodplains, whereas in uplands a hint of the savanna mode only becomes apparent around 1,000 mm.

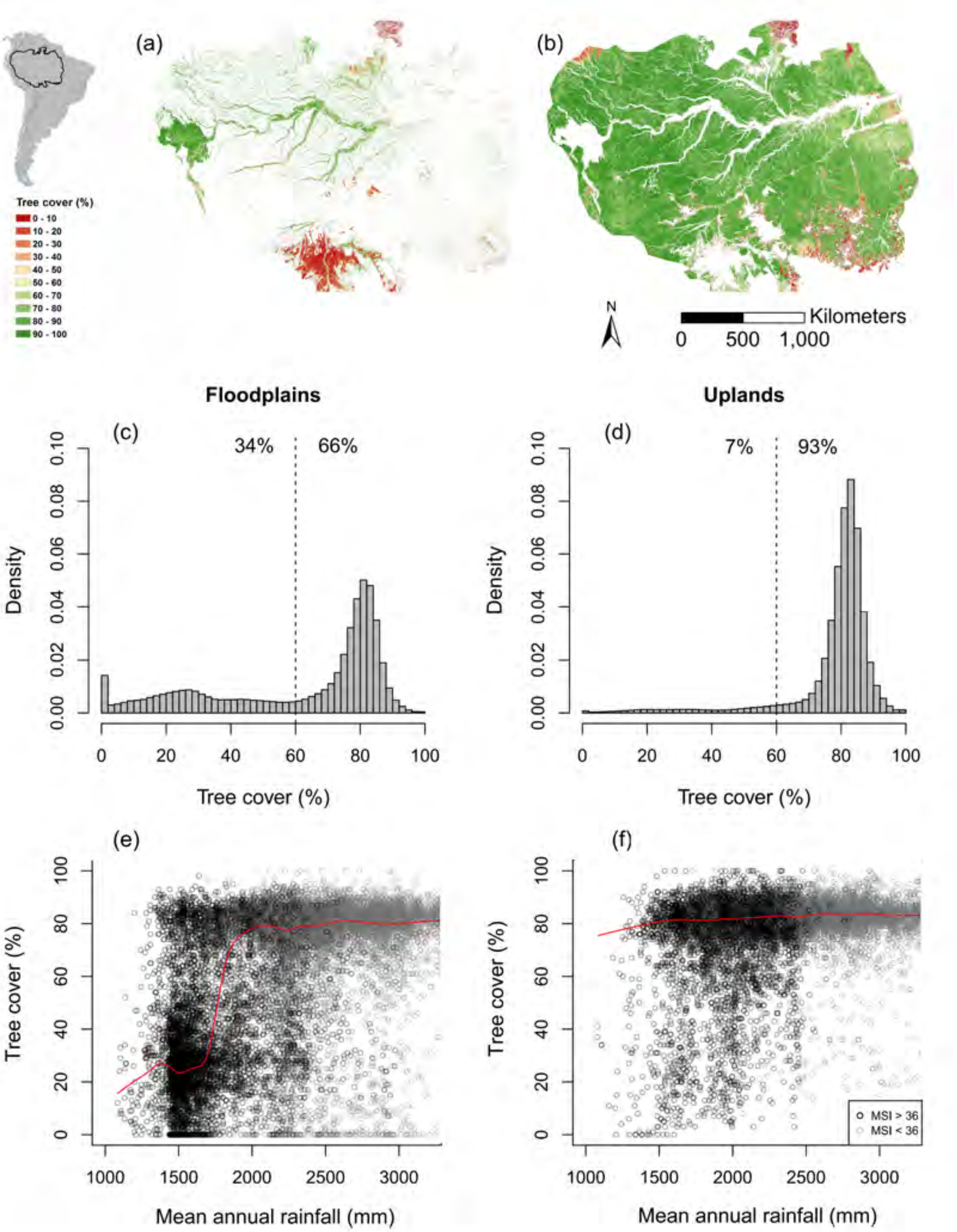

Figure 2.1. Distribution of tree cover across the Amazon and rainfall gradient. Separated by the wetlands' mask (*9*): (a), floodplains; and (b), uplands. Deforested areas were excluded (*10*). Probability density distributions of tree cover (%) for: (c), floodplains; and (d), uplands. A cutoff at 60 % tree cover (dashed lines) separates forest from savanna (*3*). Percentage values are the proportion in each state. Relation between mean annual rainfall and tree cover for: (e), floodplains; and (f), uplands. Markham Seasonality Index (MSI) values > 36 are shown by black circles, and < 36 by gray circles. Red lines are fitted LOWESS. Circles are 15,000 data points randomly sampled for each case.

Thinking of our probability densities as a long term balance between shifts back and forth, those ratios should reflect the relative likelihoods for a forest patch to shift to savanna and vice versa. Long-term tree-cover time series of sufficient quality are lacking, making it difficult to check this inference systematically. However, wildfires are the dominant mechanism driving shifts from forest to savanna (Mayle and Power 2008), and the mega-droughts of 1997 and 2005 invoked a large number of such fires in our uplands as well as floodplains (Aragão et al. 2007; Flores et al. 2014; Alencar et al. 2015). Systematic comparison reveals that in floodplain forests, fires had a stronger and longer-lasting impact than in upland forests where the effects of fires were typically small and ephemeral (Fig. 2.2 a, b; Appendix 2.6). This pattern in the tree cover dynamics that we observed with satellite was confirmed by field data on tree basal area from central Amazonia, where floodable forests recovered at much lower rates than uplands (Fig. 2.2 c, d). Even after several fire events, upland forests recovered faster than floodplain forests burnt once and twice, which implies that floodplain systems have more chance of being trapped by recurrent fires (Hoffmann et al. 2012; Murphy and Bowman 2012). Therefore, these observations are consistent with the view that transitions from forest to savanna are more likely on seasonally inundated parts of the Amazon basin than in uplands, as inferred indirectly from probability distributions (Fig. 2.1 b, c). In addition, it may well be that the backward transition from savanna to forest is less likely in floodplains as compared to uplands.

Our complementary sets of observations thus converge in suggesting that seasonally inundated forests have a markedly lower resilience than upland *terra-firme* forests of the Amazon. This raises the question of what could cause this difference. One possibility is that the structure of floodplain forests makes them more flammable (Resende et al. 2014). Upon the annual retreat of the waters, these forests have large masses of relatively dry root-mats exposed that may spread fire effectively (dos Santos and Nelson 2013) (see Appendix 2.7). Although both floodplain and upland forests can spread fires in drier years, the higher loss of tree cover in floodplains (Fig. 2.2 a, b) may contribute to hinder forest recovery in the short-term. In line with our observations, upland forests are usually found to recover swiftly upon fire (Fig. 2.2 b, d) as pioneer trees recruit into the open spaces (Barlow and Peres 2008). Another possibility is that the slower forest recovery in floodplains could be related to physiological constraints during seasonal inundation (Schöngart et al. 2002). Despite such limitation, many floodplains that inundate several months every year across the Amazon are covered by tall dense forests (Junk et al. 2011), showing that inundation alone cannot explain the distribution of forests and savannas.

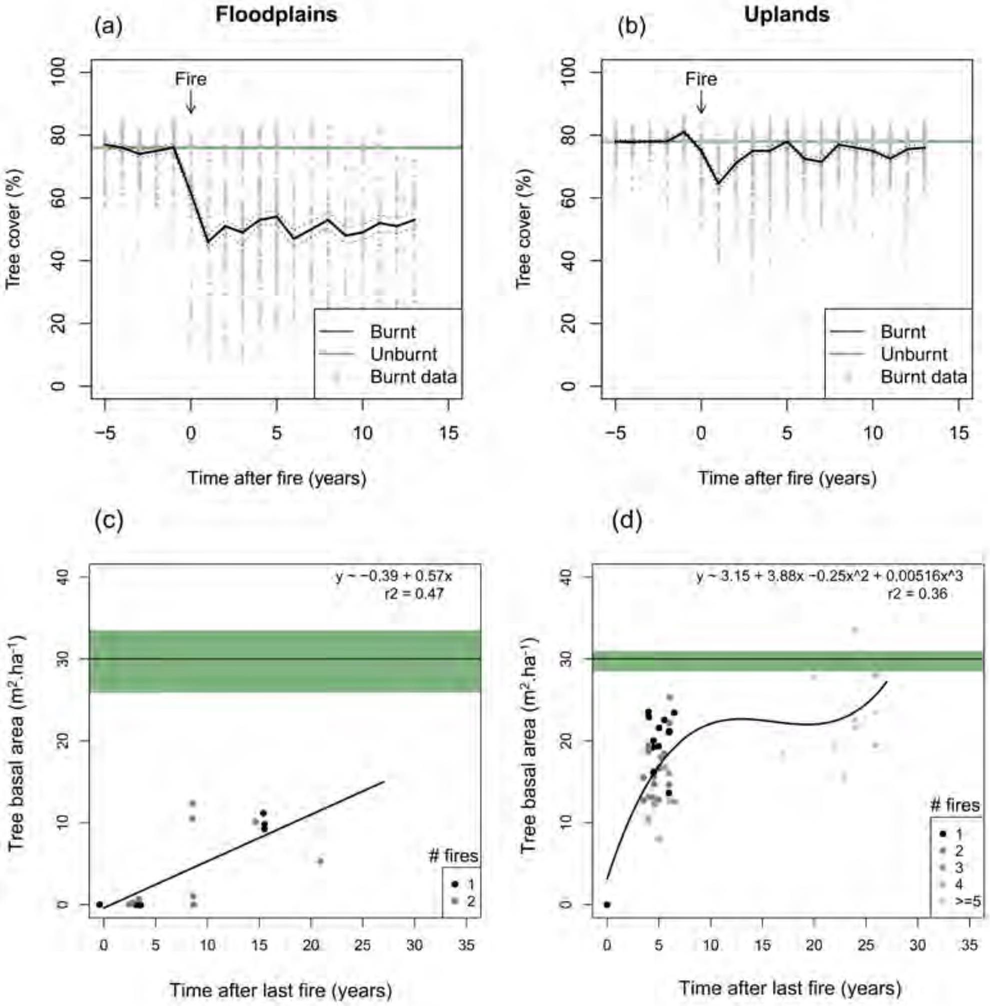

Figure 2.2. Compared sensitivity of floodplain and upland forests to fire. Satellite derived time series of annual tree cover (median ± se) and changes following forest fires for: (a), floodplains; and (b), uplands. After fire (time = 0), tree cover median persists below 50 % in floodplains, yet recovers in uplands. Field data on tree basal area recovery after the last fire in central Amazon for: (c), floodplains; and (d), uplands. Circle colors indicate number of fires. For all plots, green shaded area is standard error intervals for unburnt forests. In (d), unburnt reference was extracted from Guariguata and Ostertag (2001) (see Methods for details).

An alternative explanation for the lower resilience of floodable forests is that delayed recovery of tree cover after fire reflects the onset of a transition towards a true savanna state with a tree cover of ~ 35 %. Studies in other savanna systems suggest two mutually reinforcing mechanisms that could play a role in propagating the system through such a transition. First, increased canopy openness upon the first fire enhances the risk of subsequent fires as herbaceous plants invade and conditions under the canopy become drier (Cochrane et al. 1999). Second, soil fertility may degrade upon the loss of forest (Shakesby and Doerr 2006; Staal and Flores 2015), hindering tree recovery in the long run. Such loss of fertility could be particularly pronounced in Amazonian forests seasonally inundated by nutrient-poor waters (Junk et al. 2011). We found evidence that both mechanisms may contribute to explain the lower forest resilience on floodplains compared to uplands. In addition to the slower recovery of tree cover in floodplains, compared to uplands (Fig. 2.2), our results show that after a first fire, floodplain soils degraded continuously, whereas upland soils maintained most of the original soil conditions (Fig. 2.3). Floodplain soils eroded intensely in less than 40 years, losing clay and nutrients (phosphorous and nitrogen) important for the maintenance of forest structure (Quesada et al. 2012). In contrast, the soils of upland forests seem to be more resistant to erosion and nutrient leaching (Shakesby and Doerr 2006), despite being burnt several times in 70 years (Fig. 2.3). The more intense leaching on floodplain systems may contribute to accelerate the transition to a true savanna state. Savannas are diverse ecosystems that differ in many ways from degraded forests, and the transition would require shifts in plant composition (Veldman and Putz 2011).

Whatever the precise mechanisms may be, the patterns we revealed imply strong evidence that the floodable forests of the Amazon have a lower resilience than upland forests when it comes to the risk of transition into a fire-dominated savanna state. This has broad implications for the potential response of the Amazon basin to climatic change. For instance, some floodplains in western and central Amazonia include vast peatlands that store enormous amounts of carbon (Lähteenoja et al. 2013; Draper et al. 2014), which could potentially be released to the atmosphere by fire. Also, our analysis implies that if climate becomes drier in regions where high rainfall currently buffers fire percolation, floodplains savannas may expand, extending this fire prone ecosystem towards the resilient core of the Amazon forest (Fig. 2.1). It seems reasonable to expect that this will also affect the fire risk for upland forests. Spread of fires from floodplains to adjacent uplands has been shown in Africa (Heinl et al. 2007), and in the central Amazon (Resende et al. 2014).

Taken together, our analyses suggest that the seasonally inundated parts of the Amazon forest represent an Achilles' heel when it comes to resilience to climate change. These systems cover a substantial part of the basin (14%), and their distinctive properties make them likely starting points of fires that may percolate through large stretches of forest in dry years. In view of the expected effects of climate variability intensification on tropical regions (Holmgren et al. 2013), it follows that effective strategies to maintain a safe operating space for the Amazon forest (Scheffer et al. 2015a) may require a special attention to the floodable heart of the system.

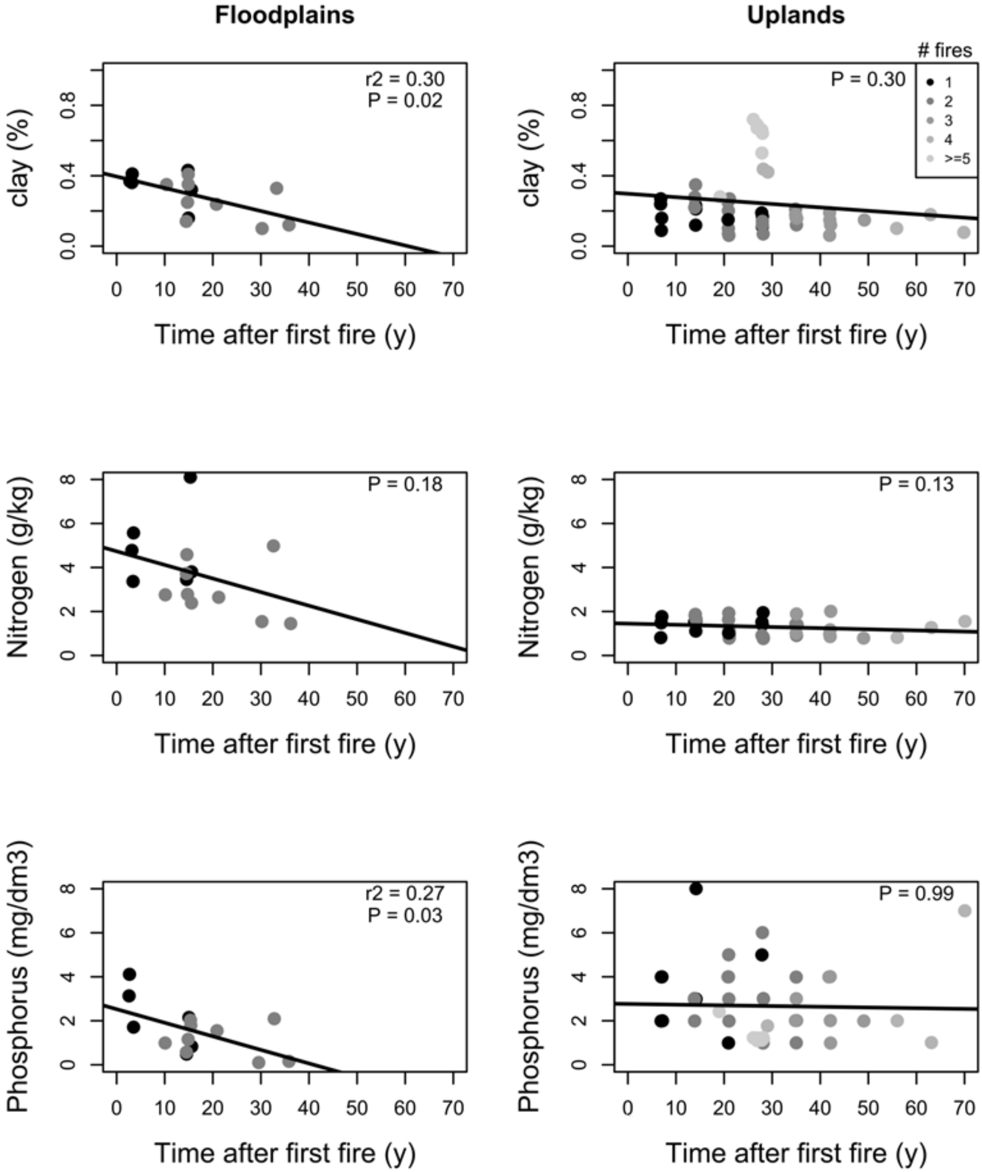

Figure 2.3 Changes in soil texture and fertility after the first forest fire. Left column: floodplain forests; and right column: upland forests. Circle gray-scale indicates number of fires.

Methods

Data description

Wetlands Mask: Uplands and floodplains were distinguished across the Amazon basin using the Amazon Wetlands' Mask (Hess et al. 2015) (from daac.ornl.gov/LBA/guides/LC07_SAR_Wetlands_Mask.html). This mask identifies areas that are permanently or seasonally covered by water (following the definition of wetland by the Ramsar Convention) at a spatial resolution of ~90 m with an accuracy of 93%. Floodplain areas were extracted by comparing the remotely-sensed images of Japanese Earth Resources Satellite (JERS-l) between the low water season of 1995 and the high water season of 1996 when the wetlands' mask was produced. The mask does not include the Tocantins watershed and most of the Amazon estuarine islands that are part of the lower Amazon basin. Permanent water bodies were excluded.

Tree cover: The 250-m resolution MODIS vegetation continuous field (VCF) Collection 5 dataset for the year 2001 (DiMiceli et al. 2011) was used to analyze the tree cover distributions of the Amazonia uplands and floodplains, respectively. For the analysis of tree cover recovery after fire, annual MODIS VCF tree cover data between 2000 and 2010 were obtained for each study site (Appendix 2.2).

Rainfall: Mean annual precipitation (MAP) data at 1 km^2 resolution (Hijmans et al. 2005) were downloaded from the WorldClim website (http://www.worldclim.org/current). This dataset is interpolated from monthly averages of precipitation obtained from weather stations between 1950 and 2000.

Deforested areas: We excluded all areas deforested until 2014 obtained from the deforestation project PRODES for the Brazilian Amazonia (http://www.dpi.inpe.br/prodesdigital/prodes.php). This project mapped annual deforestation since 1988 with the use of Landsat TM images to be used by the Brazilian government. We also excluded the lower Amazon River floodplains because of the long history of human land-use (Reno et al. 2011), and to exclude floodplains under tidal influence.

Fire detection: We analyzed the recovery of tree cover after wildfires in floodplain and upland forests across the Amazon basin. Although signs of fire in the forest canopy can be ephemeral, lasting for one or two years (Supplementary Fig. 3), it is possible to use Landsat imagery for forest fire detection at a much finer resolution of 30 m (Alencar et al. 2015). We selected eight Landsat scenes covering most of the annual rainfall gradient (Appendix 2.1), and obtained of cloud-free images for the years before and after 1997 and 2005. Both years had strong droughts and wildfires penetrated closed forests in different parts of the Amazon basin (Aragão et al. 2007; Flores et al. 2014; Alencar et al. 2015). We selected the burnt/unburnt sites through visual identification to ensure these sites were burnt by wildfires that spread during periods of extreme drought. This way we avoided areas burnt intentionally for land use for instance that can be easily identified by their straight borders, compared to rounded borders of wildfire scars. Fire scar edges were avoided by selecting sites located at least 1 km from the border with unburnt forests. In large scars, the selected sites are spaced by at least 2 km.

Field data: To validate the remote sensing analysis of tree cover recovery after fire, we analyzed data on tree basal area from secondary forests recovering after being burnt in floodplains and uplands of central Amazonia (Appendix 2.1). For floodplains, we used 15 sites burnt by one or two wildfires that penetrated different forests. Three unburnt floodplain forests were used as reference. These sites are spread within 50 km of the town of Barcelos, State of Amazonas, Brazil, in the Negro river basin. For uplands, we used burnt sites from two different sub-basins the Negro and the Solimões. The first is located north of Manaus, includes 17 forests abandoned from slash-and-burn agriculture and pasture with fire management, and has been studied for more than 30 years by the Biological Dynamics of Forest Fragments Project (BDFFP). The other is located in the lower Tefé river and includes 33 forests abandoned from slash-and-burn agriculture. In those sites abandoned after several cycles of land-use with fire, we followed the recovery of tree basal area after the last fire to validate the satellite study. For upland unburnt forest reference on tree basal area, we extracted data from one published review (Guariguata and Ostertag 2001).

Field soil data: Using all these secondary forests described above, we produced three different chronosequences to analyze changes in soil texture and fertility following the first fire.

Description of floodplains and uplands

Amazonian floodplains are formed by different types of tropical wetlands, with varying flooding duration lengths, water chemistry, and vegetation types (Junk et al. 2011). In these aquatic-terrestrial zones, plants have special adaptations to cope with the annual floodpulse. These ecosystems cover together 14% of the Amazon basin (Hess et al. 2015), but are mostly spread across the central-western regions (Fig. 2.1 a). Floodplain landscapes, as well as adjacent uplands, have been used by human populations since pre-Columbian times for being close to settlements (Clement et al. 2015). Therefore, the vegetation along the major Amazonian rivers may have a long fire history. Floodplain forest fires can have drastic consequences for biodiversity, as suggested for instance by persistent shifts in bird composition (Ritter et al. 2012).

Uplands of the Amazon, or *terra-firme*, are lands not floodable by rivers or accumulated rainfall. They cover 86 % of the Amazon basin (Fig. 2.1 b). Palaeo-ecological evidence suggests that most of the Amazon remained forested during the last 8,000 years, and that only in peripheral transition zones biomes expanded (Mayle and Power 2008), in part due to pre-Columbian human activities (Clement et al. 2015). Recently, Amazonian uplands have been intensely deforested (more than 15 % of all forests) (Malhi et al. 2008), especially from the south-eastern portions known as “arc of deforestation”. However, other human activities have also contributed to degrade Amazonian forests, such as logging, fragmentation and road construction, making these more susceptible to drought-driven fires (Malhi et al. 2008).

Analyses of tree cover distribution

We analyzed the frequency distributions of tree cover, and the relationship between tree cover and rainfall in Amazonian floodplains and uplands. The significant number of modes in tree cover distributions for floodplains and uplands was tested with latent class analysis that fits normal frequency distributions to the data, using R package FlexMix (R 3.2.1, FlexMix version 3.2.2). The number of modes is quantified based on the most parsimonious model through an expectation-maximization procedure. Bayesian Information Criterion (BIC), the Akaike Information Criterion (AIC) and the Integrated Completed Likelihood (ICL) criterion were used for model selection. The tree cover data were arcsine square-root transformed to approach normal distributions. We randomly sampled 15,000 points for each ecosystem type. The result of the analyses reveals two modes for floodplains and two for uplands (Appendix 2.3). For uplands, the mode that peaks at 67 % tree cover overlaps with the major forest mode that peaks at 84 % tree cover. We interpret this mode as overfitting of the long tail that may reflect deforested or degraded areas that we were not able to exclude completely. Hence we only consider two modes for floodplains and one mode for uplands (Fig. 2.1), with cutoffs at 60 % (Hirota et al. 2011). The computed potential landscapes of floodplains and uplands (Appendix 2.5) show basins of attraction for each ecosystem based on the potential analysis (Livina et al. 2010).

We also explored the role of the extensive floodplain savanna in the Bolivian south of the Amazon (Llanos de Moxos), and of the extensive floodplain forest in Peru (Marañon-Ucayali basins) in the bimodality of Amazonian floodplains (Appendix 2.8). When removing the extensive Bolivian savanna, the floodplain savanna mode reduces. Nonetheless, frequencies of tree cover below 60 % still remain higher than the frequencies observed in uplands (Fig. 2.2 b). Moreover, these extensive floodplain savannas are also at the drier extreme of the annual rainfall gradient (below 1,500 mm.y^{-1}), which may be a tipping point for the stability of floodplain forests.

Analyses of tree cover after fire

Using the MODIS VCF annual data (DiMiceli et al. 2011) between 2000 and 2010 we analyzed tree cover changes after fires in floodplain and upland forests. Although the 1997 and 2005 fires occurred more frequently in different regions (Appendix 2.2), the response of tree cover was similar (Appendix 2.9), and thus we analyzed both time-series as one (Fig. 2.2 a,b).

Inter-annual MODIS VCF data have been suggested as not appropriate to synoptically document annual change due to the uncertainties arising from clouds and other factors (Carroll et al. 2011). In our case, however, changes in tree cover after fire largely exceed the inter-annual data variation (Appendix 2.9), showing that our analysis based on change detection is clearly robust to the data noise in the product.

Acknowledgments

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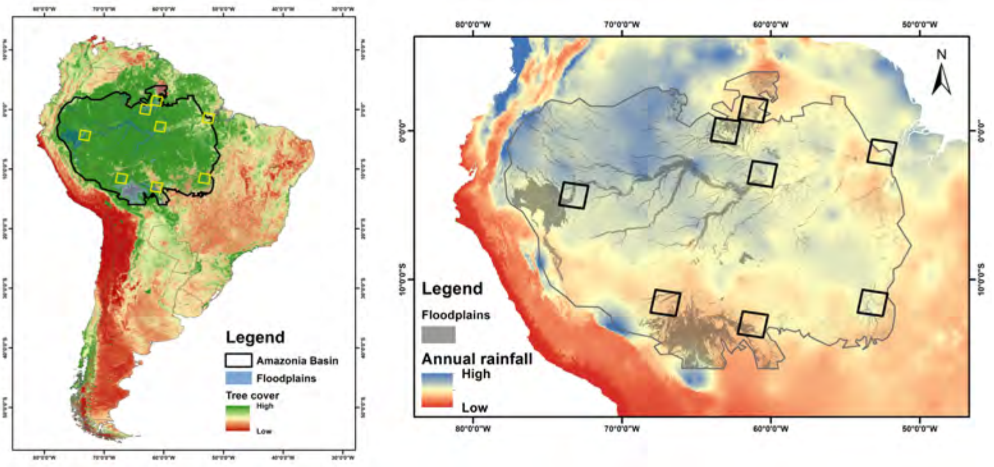
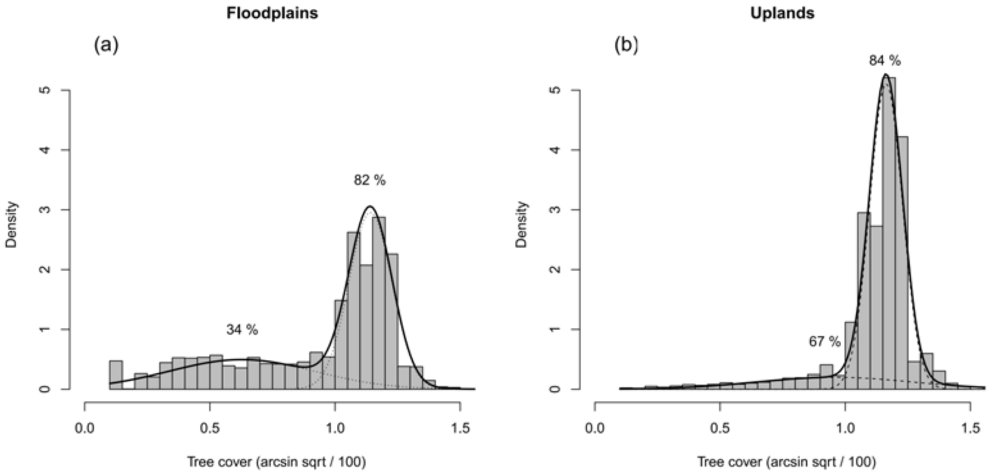
Appendices



Appendix 2.1. Maps with sites selected to study wildfires. Left map shows tree cover for South America. Right map shows floodplains, and mean annual rainfall. Black squares show Landsat scenes chosen to represent floodplains and uplands systems across most of the rainfall gradient. Locations of field sites used for the fire study are indicated by red circles for uplands, and blue circle for floodplains.

Appendix 2.2. Number of sites selected in each Landsat scene. In these sites we studied tree cover change after the 1997 and 2005 fires (see Fig. 2.2 a,b; and Methods for details).

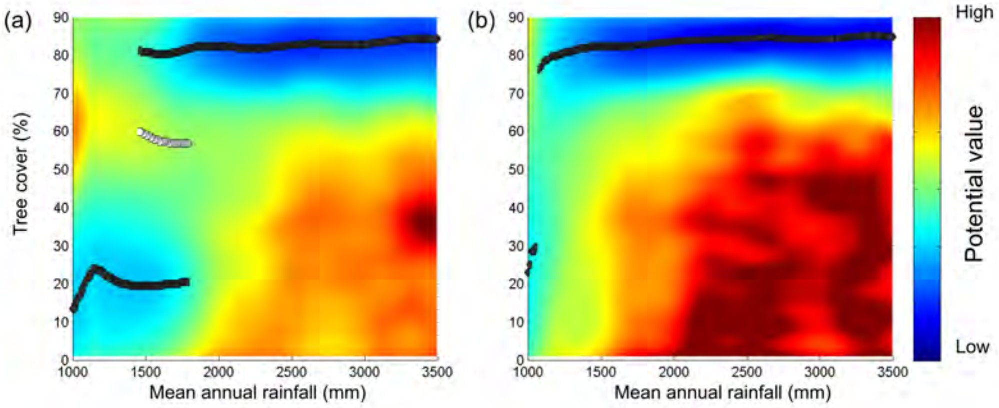
Region	Landsat scene	Ecosystem	Burnt in 1997	Burnt in 2005	Unburnt
South	230/69	Upland	3	9	6
		floodplain	6	22	6
South East	225/68	Upland	10	16	6
		floodplain	5	5	6
South West	001/68	Upland	21	48	6
		floodplain	4	37	6
North	232/59	Upland	39	0	6
		floodplain	21	0	6
Central	231/62	Upland	12	0	6
Central-North	233/60	floodplain	11	0	6
East	226/61	Upland	0	0	6
		floodplain	0	7	6
West	006/63	Upland	0	0	3
		floodplain	4	6	6
Amazonia		Upland	85	73	39
		floodplain	51	77	42



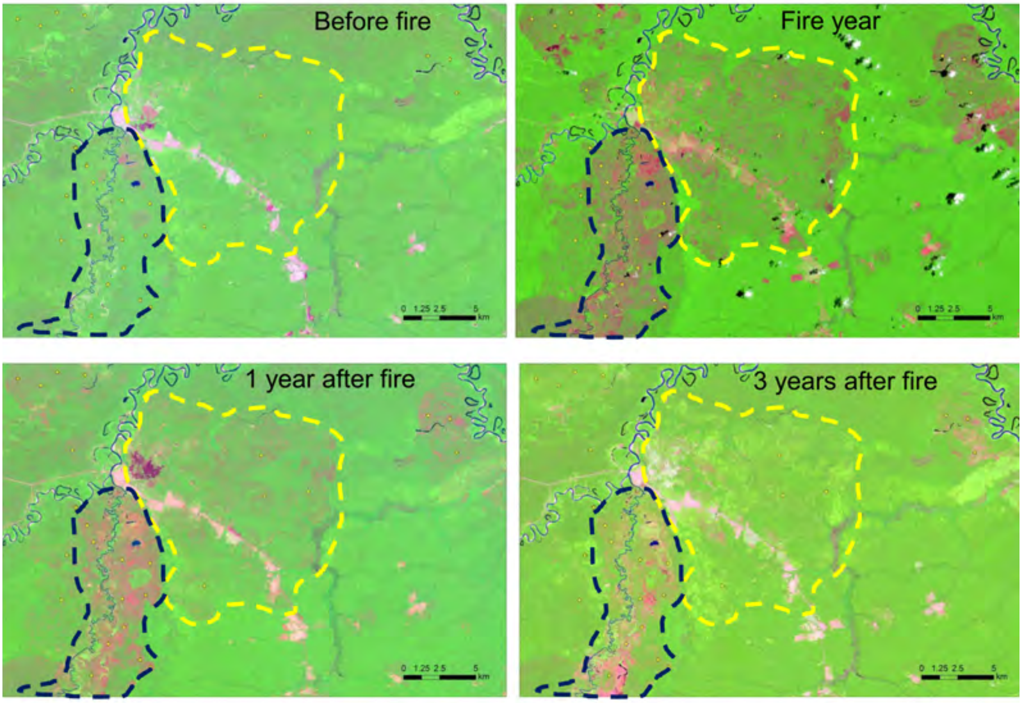
Appendix 2.3. Probability density distributions of tree cover across the Amazon. (a), floodplains; (b), uplands. Percentage values indicate tree cover at the peaks of each mode. The mode that peaks at 67 % tree cover in uplands is due to over fitting of the long tail, and likely represents secondary forests.

Appendix 2.4. Proportion of floodplains and uplands covered by forest and savanna (tree cover cutoffs at 60%). Areas calculated with wetlands' mask (Hess et al. 2015), excluding deforested areas (see Methods).

Ecosystem	Forest (%)	Savanna (%)	Area (km^2)	Forest area (km^2)	Savanna area (km^2)
Floodplain	66	34	816,200	538,692	277,508
Upland	93	7	5,013,800	4,662,834	350,966
All Amazon	89	11	5,830,000	5,201,526	628,474

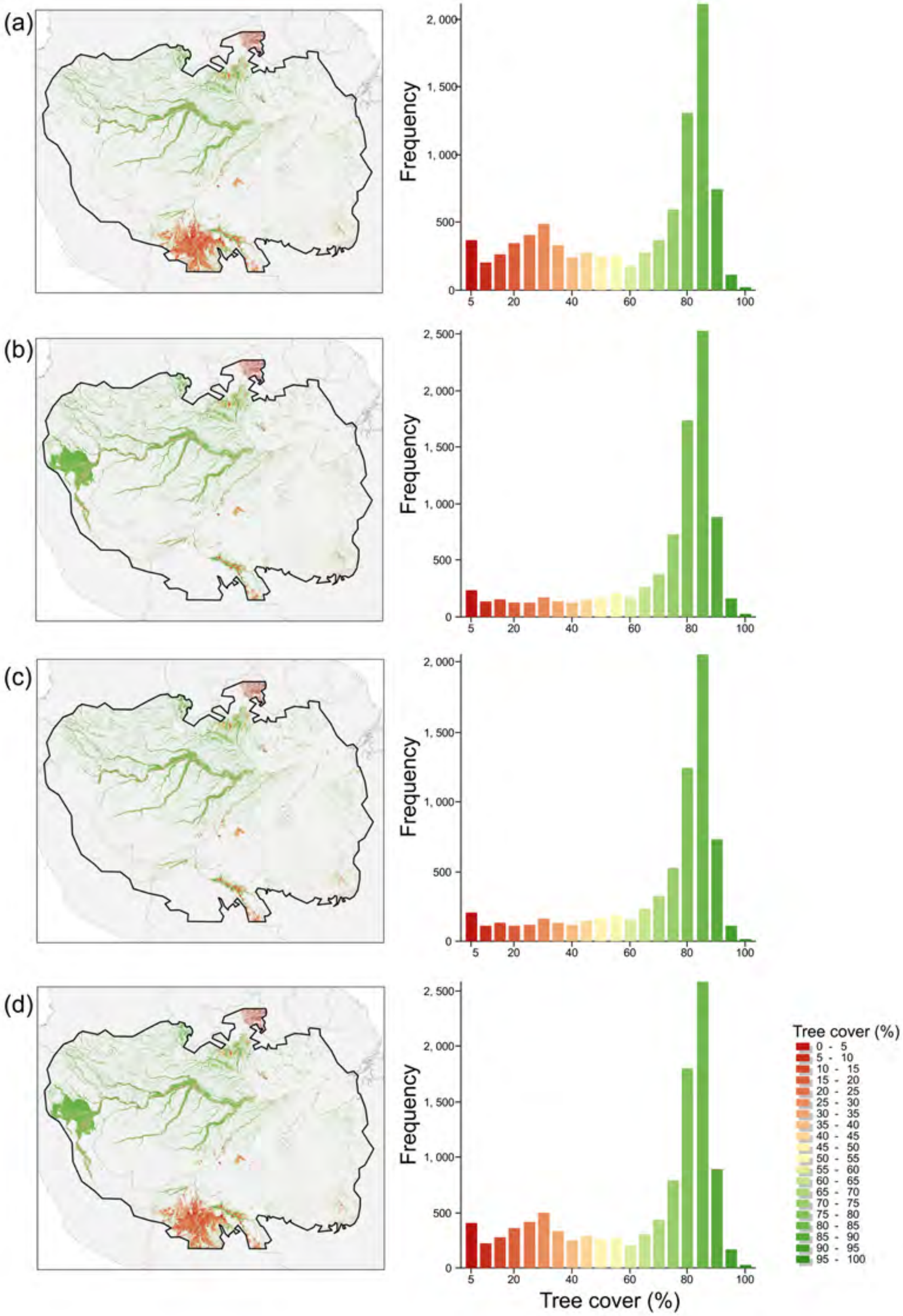


Appendix 2.5. Computed landscapes of probability densities for the Amazon, based on potential analysis (Livina et al. 2010). (a), floodplains; (b), uplands. Blue areas approximately represent the basins of attraction; black dots represent the minima and white dots the maxima, as the stable and unstable states respectively.

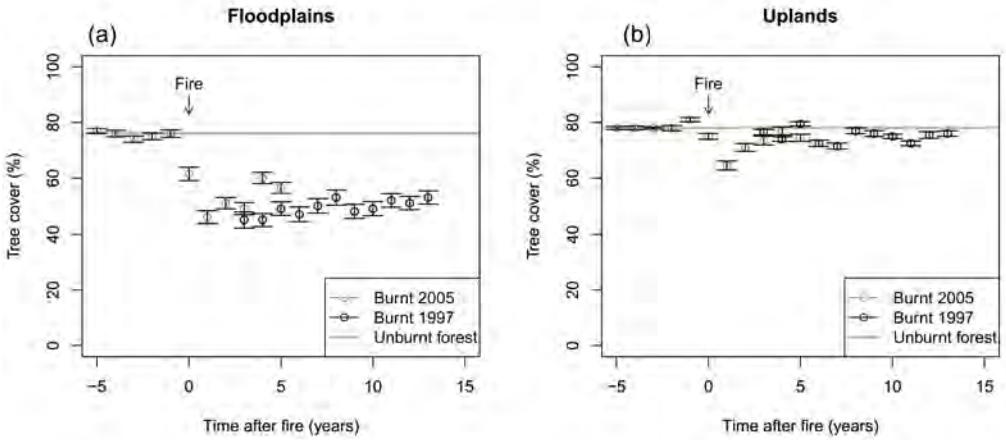


Appendix 2.6. Example of study sites burnt in 2005 shows how quickly signs of fire disappear. Landsat TM images from Bolivian rainforests (scene 001/68, pseudo-color combination of bands 5, 4 and 3 for channels red, green, and blue). Forests are shown in green and burnt areas in magenta. Dashed lines indicate: blue, floodplains; yellow, uplands.

Appendix 2.7. Floodplain forests and fire. (a), floodplains of the Jari river, Purus sub-basin; (b), root mat above the soils of blackwater floodplain forests; (c), fireman trying to stop a floodplain fire at the Anavilhanas National Park, Negro river, during the extreme drought of late 2015; (d), Floodplain forest three years after a first fire at the middle Negro river. Photo credits to: (a), Diogo Lagroteria; (b), Aline R. dos Santos; (c), Enrique Salazar (ICMBio/ PARNA Anavilhanas); (d), Bernardo M. Flores.



Appendix 2.8. Maps and frequency distributions of tree cover for Amazonian floodplains. (a), Large forest in Peru (Marañon-Ucayali) excluded; (b), large savanna in Bolivia (Llanos de Moxos) excluded; (c), large forest and large savanna excluded; (d), all floodplains.



Appendix 2.9. Annual tree cover (median ± se) for burnt forests. (a), floodplains; (b), uplands. Green stripe indicates standard error intervals for unburnt forests in each ecosystem. Data was obtained for the period between 2000 and 2010 for both burnt and unburnt sites (see Methods for details).

Chapter 3

Repeated fires trap Amazonian blackwater floodplains in an open vegetation state

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Abstract

Climate change may increase the occurrence of droughts and fires in the Amazon. Most of our understanding on how fire affects tropical ecosystems is based on studies of non-flooded forest-savanna ecotones. Nonetheless, tropical floodplain forests in Amazonian can burn severely during extreme droughts. The mechanisms slowing down forest regeneration in these ecosystems remain poorly understood and have never been assessed in the field.

We studied the recovery of Amazonian blackwater floodplain forests after one and two fire events. We used Landsat images to map fire history and conducted field surveys to measure forest structure, tree species richness, tree seed bank, and post-fire invasion of herbaceous plants.

Sites burnt once had on average 0% trees, 6% tree seed abundance, 23% tree seed species richness, and 8% rootmat thickness compared to unburnt forests. In contrast, herbaceous cover increased from 0 to 72%. Nonetheless, forest structure and diversity recovered slowly towards pre-burn levels, except for tree seed banks that remained depleted even 15 years after fire.

Sites burnt twice had on average 0% trees, 1% of tree seed abundance, 3% of tree seed species richness and 1% of rootmat thickness compared to unburnt forests. Herbaceous cover increased to 100%. Mean recovery of tree basal area was 50% slower, and of rootmat thickness 93% slower compared to recovery in sites burnt once. Tree seed banks did not recover at all, and herbaceous cover persisted close to 100% for more than 20 years after second fire.

Synthesis and applications. Our results indicate that after a second fire event, blackwater floodplain forests lose their recovery capacity, and persist in a non-forested state dominated by herbaceous vegetation. Such fragility implies that preventing human ignited fires during drought episodes is a particularly important conservation strategy for these ecosystems.

Introduction

Fire can limit the distribution of tropical forests, allowing savannas to expand in regions where precipitation levels could support higher tree cover (Bond, Woodward & Midgley 2005; Sankaran *et al.* 2005; Staver, Archibald & Levin 2011; Dantas *et al*. 2015). Most of our understanding on how fires shape tropical terrestrial ecosystems, however, comes from forest-savanna borders in upland (non-flooded) areas. In these transition zones, many tree species have adaptations to tolerate fire (Dantas, Batalha & Pausas 2013).

However, recurrent fires can arrest forest succession when soil nutrient conditions are too low for trees to grow fast and escape the next fire (Lehmann *et al.* 2011; Grady & Hoffmann 2012; Hoffmann *et al.* 2012). In the wet undisturbed uplands of the Amazon, forests usually have low resistance to fires (Uhl & Kauffman 1990; Brando *et al*. 2012). When these forests become more flammable in dry years (Aragão *et al*. 2007; Alencar *et al*. 2015) up to 42% of trees can be lost to fire (Barlow & Peres 2004). Nonetheless, a closed canopy forest usually regenerates, even after several fire events, with tree communities dominated mostly by pioneer (Barlow & Peres 2008), fire-tolerant (Veldman & Putz 2011), and resprouting forest species (Jakovac *et al*. 2015).

Forest recovery following disturbances can be limited by multiple mechanisms (Chazdon 2014). For instance, the capacity to tolerate fire differs across species, thus affecting the species composition of regenerating forests (Kauffman 1991; Hoffmann 1998; Bond & Midgley 2001; Pausas & Bradstock 2007). The establishment of new individuals can be constrained by seed availability (Uhl 1987, Nepstad *et al.* 1996, Kennard *et al.* 2002), and factors that limit seed germination and seedling survival (Hoffmann, Orthen & Franco 2004, Acácio *et al.* 2007, Bond 2008). Moreover, expansion of herbaceous vegetation can limit tree recruitment by direct resource competition, or by promoting the spread of new fires (Bond 2008, Hoffmann *et al.* 2009). Fire also modifies soil properties and favors the release of nutrients stored in the trees and organic layer, which later can be leached out of the system (Kauffman *et al*. 1995; Certini 2005), limiting even more tree recruitment (Hoffmann *et al*. 2012; Murphy & Bowman 2012).

In dry years, tropical floodplain forests can burn severely (Page *et al.* 2002; Flores, Piedade & Nelson 2014; Maracahipes *et al.* 2014; Resende *et al*. 2014). In the Amazon, satellite images of the Negro river indicate that burnt floodplain forests recover at a much lower rate when compared to burnt upland forests (Flores, Piedade & Nelson 2014). These floodplain forests can lose 88% of tree cover when burnt during dry El Niño events that prolong the low water season. The massive tree mortality during fire and the slow recovery of floodplain forests afterwards suggest that these ecosystems could be trapped by fire in a non-forested state if burnt repeatedly.

In this study we assessed the capacity of blackwater forests to regenerate after being burned repeatedly (Fig. 3.1). We hypothesized that each fire event can lower the capacity of floodplain forests to recover by destroying trees, tree seed banks and root-mats, and by favoring the expansion of herbaceous cover (herbs and graminoid vegetation). Blackwater forests are extensive in the lower and middle Negro river, but also occur along most tributaries of Amazonian rivers (Junk et al. 2011). Despite the low nutrient availability in these systems, forests can attain high biomass (Schöngart & Wittmann 2010) that supports most of the aquatic food chain (Henderson 1990). Hence, these forests are crucial for maintaining fishery activities by local human populations (Saint-Paul et al. 2000). This ecosystem also hosts extensive peatlands as a potential carbon source if burnt (Lähteenoja, Flores & Nelson 2013), yet despite its high natural flammability, most blackwater forests across the Amazon remain unprotected.

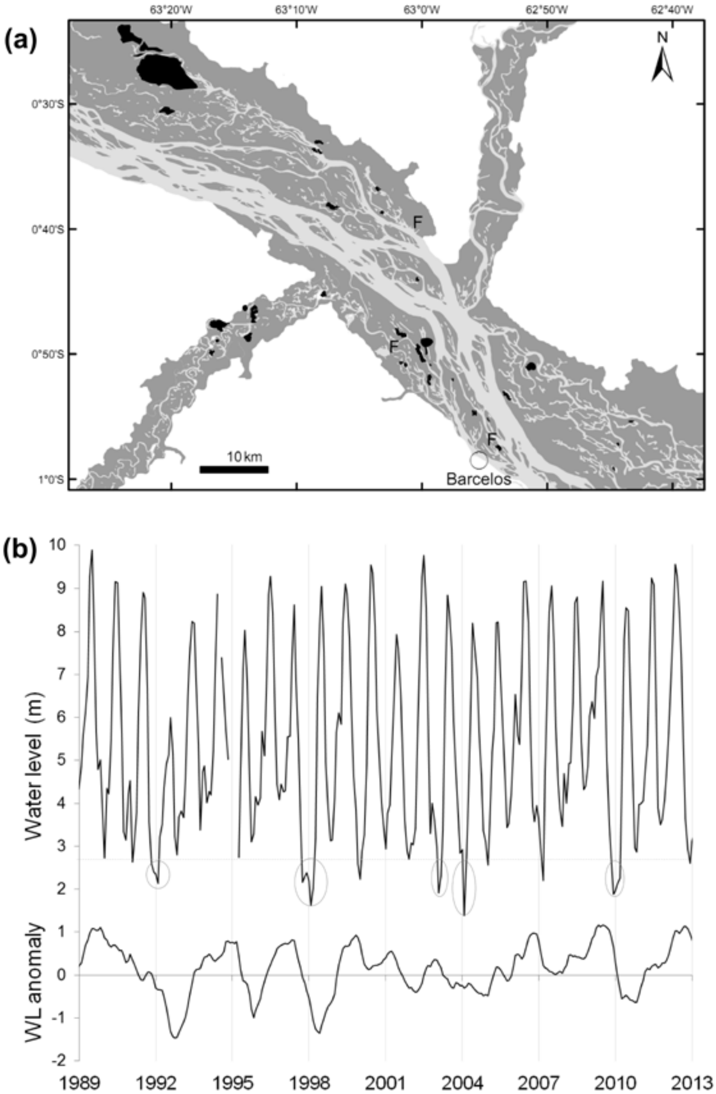

Figure 3.1. Dry years and floodplain fires on the middle Negro river; (a) floodplains are dark grey, open water is light grey; fire scars burnt from 1973 to 2012 are black (48% of these burned twice in this period), fire scars we studied are red, mature forest study sites are marked ´F´; (b) Time-series of the water level measured daily at town of Barcelos, red circles indicate fire years.

Materials and methods

Study system

We studied floodplains of the middle Negro river and tributaries located within 50 km of the town of Barcelos, Brazil, (0^{o}58S, 62^{o}55W). A predictable annual floodpulse of 5.5 m mean amplitude reaches its lowest level in January and highest in July, inundating the floodplains with acid (pH 3.5–4.0) and nutrient-poor blackwater (Junk *et al.* 2011). Near Barcelos, mean annual precipitation is 2100 mm, with over 100 mm month^{-1} during the whole year. Floodplains of this region form along ca. 200 km of the Negro river, the Mariuá archipelago, that represents the world's most extensive, yet unprotected area of blackwater forests.

Blackwater forests typically have a rootmat that protects the soil organic layer, allowing trees to recycle nutrients that would otherwise be leached by annual floods (Stark & Jordan 1978, Singer & Araujo-Aguiar 1986). In the Negro river basin for instance, root mats have been found in 63% of floodplain forests, but in only 11% of upland forests (dos Santos & Nelson 2013). On the other hand, root mats increase the flammability of blackwater forests in dry years (Flores, Piedade & Nelson 2014). These floodplain fires can accidentally leak from camp-fires and nearby upland agricultural sites.

Site selection

Using Landsat images for the period 1973-2012, we identified 27 burn scars within 50 km of Barcelos town, of which 13 (48%) burned a second time during this period. We selected 15 burnt sites, based on the number of times they had been burnt and the time passed since the last burn (Table 3.1, Appendix 3.1). Three unburnt mature forests in this same floodplain landscape were chosen as reference plots (Fig. 3.1 a). We identified the first fire on Landsat images when a spectral pattern typical of forest canopy was transformed into open water during high water months and bare soil during low water months. A second burn inside an existing fire scar cannot always be determined directly from satellite images, but fire scar expansion is easily detected. So, when a burn scar expanded we assumed re-burning of the old portion. When a burn scar covered with light green regenerating vegetation returned persistently to bare soil spectral signature, we also inferred that site had reburned (Appendices 3.2, and 3.3).

We sampled in total 18 sites: six once-burnt, nine twice-burnt, and three mature forests as unburnt reference (Fig. 3.1 a, Table 3.1). Our burnt sites were assumed to resemble unburnt forests before they burned. At each site, we established plots of 0.6 ha (150 x 40 m). Plots in burnt sites were placed at least 30 m from the borders with unburned forest, and all plots were placed at least 100m from river channels. Long narrow plots allowed us to better control for topographic variation, thus maintaining constant dry phase length (Table 3.1).

Vegetation data

Basal area and species richness of trees e 1 cm in diameter at breast height (DBH) were obtained for all trees located within 2 m, 20 m, or 40 m, of the 150 m long center line, for DBH classes of 1-10 cm, 10-30 cm, and > 30 cm, respectively. We first identified trees to the genus level with the help of a parataxonomist, and later separated in species using the virtual herbariums from INPA, species Link, and Neotropical Herbarium.

Tree seed banks were examined in three samples collected at 50 m intervals along the center line of each plot by taking a core of 10 x 15 x 5 cm (length x width x depth) including the surface litter and root mat, for a total of 3 sub-samples per plot. From each sub-sample, we counted the number of seeds and distinguished the morphospecies with the help of a parataxonomist, for all seeds that were intact (not destroyed by fire or predators). Tree seed banks were not analyzed in the three old twice burnt sites (Table 3.1), and therefore we only infer on seed bank recovery up to nine years after the second fire.

Root mat thickness was measured at six positions (every 25 m) along the 150 m centerline of each plot. Thickness was measured with a ruler in small trenches, including the layer of very fine roots and organic humus forming the mat. Root mat thickness was easily identifiable because of the strong mechanical structure that resembled a carpet.

Herbaceous cover (graminoids and herbs) was sampled at six positions (every 25 m) along the 150 m centerline of each plot. We classified for presence or absence and then calculated the percentage that was covered with herbaceous vegetation for each plot.

Dry phase length

Dry phase length per plot was averaged from three to five measurements of water column depth on a known date in the high water season. The depth of the water column was then compared to the water level recorded at the Barcelos gauge station on the same day, and the average number of days per year that each plot stayed above water (Table 3.1) was derived from the annual curve using the historical data. Historical precipitation and water level data for Barcelos (1968 - present) was obtained from the *Agência Nacional de Águas* (http://hidroweb.ana.gov.br/).

Statistical analysis

To assess changes in vegetation after each fire event, we used as response variables: (1) tree basal area; (2) tree species richness; (3) tree seed abundance in the soil seed bank; (4) tree seed richness in the soil seed bank; (5) root mat thickness; and (6) herbaceous cover. Our explanatory variables were: (1) number of fires: one or two; (2) time since the last fire; and (3) average length of the dry phase. For each burning condition we had three replicated plots. For once burnt, we sampled sites burnt 3 and 15 years before. For twice burnt, we sampled sites burnt the last time 3 and 9 years before, plus three other sites that were burnt a second time between 9 and 21 years before, yet a first time much earlier than the other sites ~ 30 years before (Table 3.1).

To assess changes in the recovery capacity, we compared the recovery rates of the vegetation variables following each fire event. As an indicator of the recovery rate, we used the slope (partial regression coefficients) of “time since last fire” between 3 and 15 years for once burnt, and 3 and 21 years for twice burnt. We did this for each response variable using separate regressions for once and twice burnt to compare the slopes. Our regression models had two predictors: “time since last fire” and “average length of the dry phase”, to account for the effects of flooding on forest recovery. To compare slopes of “time since last fire” vs. vegetation variables (recovery rates), we used bootstrap techniques with 1,000 randomizations to obtain the uncertainty of the slopes expressed as confidence interval (CI) of the mean. For this we used package Boot for the statistical software R version 2.13.1 (R Development Core Team 2011). This way we were able to compare the recovery rates after one and two fire events (Appendices 3.5-7).

Table 3.1. Fires and dry phase lengths for floodplain sites. Sampling conducted in 2013.

Site	Number of fires	Fire dates	Time after last fire (y)	Dry phase (days.y^{1})
BA	1	2010	3	130
BB	1	2010	3	172
BC	1	2010	3	172
B9	1	1998	15	133
B10	1	1998	15	163
B13	1	1998	15	133
B3	2	1998 / 2010	3	180
BD	2	2003 / 2010	3	165
BE	2	1992 / 2010	3	172
B4	2	1998 / 2004	9	60
B7	2	1998 / 2004	9	190
BAN	2	1998 / 2004	9	197
B20	2	1980 / 1992	21	30
B83	2	1983 / 2004	9	202
B77	2	1977 / 1998	15	205
Forest 1	0	•	•	•
Forest 2	0	•	•	•
Forest 3	0	•	•	•

Results

Compared to unburnt forests, sites burnt once had on average 0% of trees, 6% of tree seed abundance, 23% of tree seed species richness and 8% of root mat thickness (Fig. 3.2). Compared to unburnt forests, sites burnt twice had 0% of trees, 1% of tree seed abundance, 3% of tree seed species richness and 1% of root mat thickness (Fig. 3.2). Herbaceous cover increased in average from 0% in unburnt forest, to 72% after first fire, and 100% after second fire (Fig. 3.2).

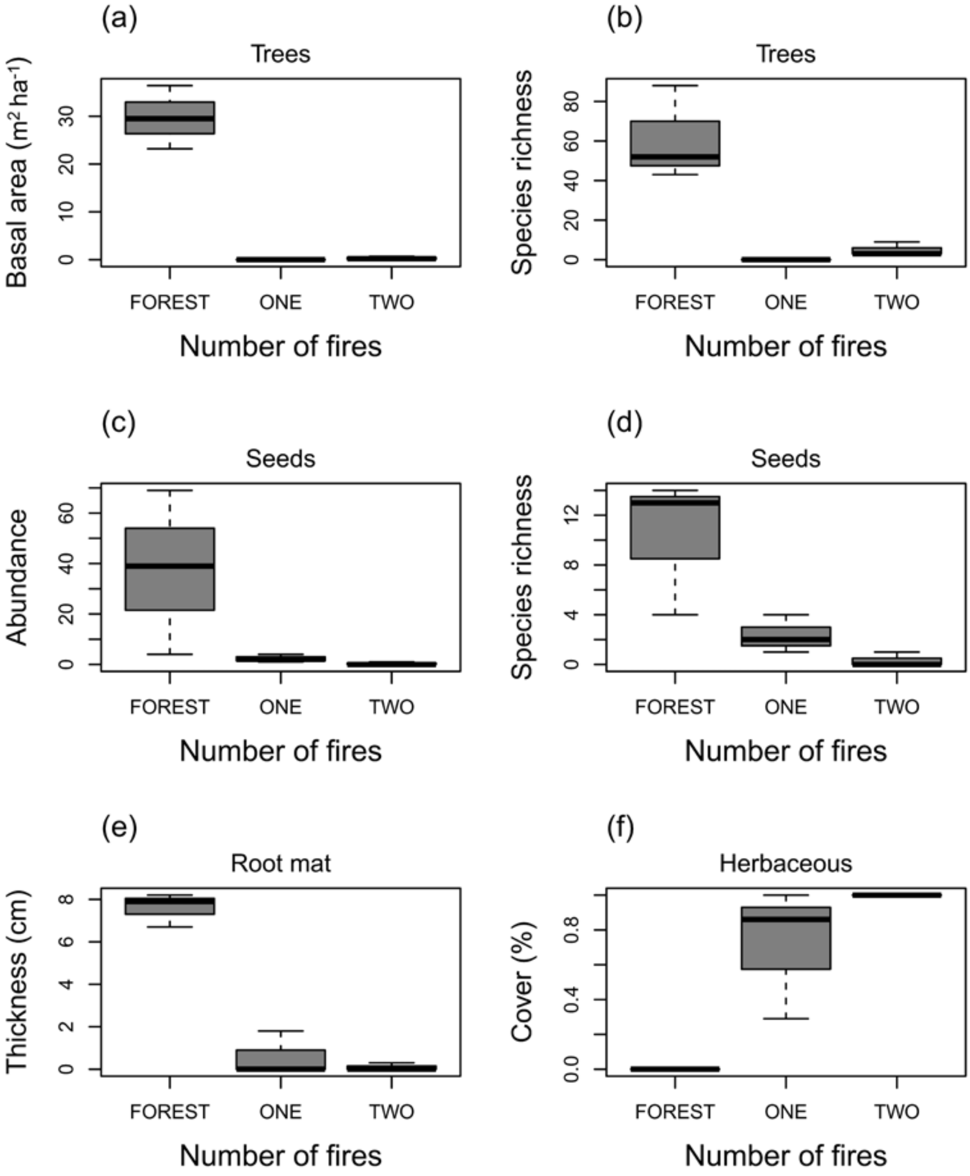

Figure 3.2. Vegetation state of unburnt forests, and of sites burnt once and twice (N = 3 for each case). We only included here plots recently burnt, thus 3 years after last fire (see Table 3.1).

In sites burnt only once, we found that tree basal area, tree species richness, and root mat thickness recovered slowly but progressively (Fig. 3.3). Recovery rates of the seed bank, however, were not different from zero (Fig. 3.3). Herbaceous cover dropped quickly towards forest levels (Fig. 3.3, Fig. 3.4 b). For sites burnt once, length of the dry phase had no significant effect on the recovery of any vegetation response variable (Appendix 3.4).

In sites burnt twice, in contrast, the mean recovery rates of tree basal area and root mat thickness dropped 50 % and 93% respectively, compared to sites burnt once (Fig. 3.3 a, e). The variance around the mean recovery rate of tree basal area and tree species richness increased, suggesting higher variation in tree recruitment in sites burnt twice, compared to sites burnt only once (Fig. 3.3 a, b). The seed bank did not recover at all (Fig. 3.3 c, d). Herbaceous cover also did not return to the pre-burn low values, as in sites burnt once (Fig. 3.3 f), and persisted at 100% for up to 21 years after the second fire (Fig. 3.4 c). Although trees recruited after the second fire, the persistence of high herbaceous cover contrasts sharply with the patterns we observed in once burnt sites (Fig. 3.4). For sites burnt twice, length of the dry phase had no significant effect on the recovery of any vegetation response variable (Appendix 3.4).

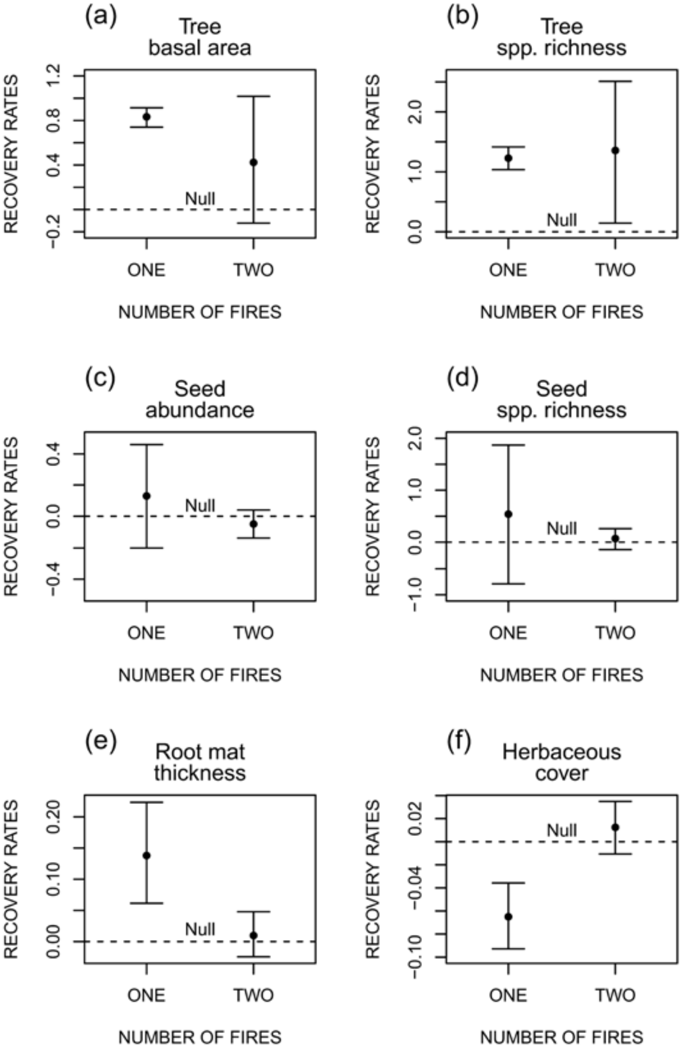

Figure 3.3. Recovery rates of the vegetation following one and two fire events. Horizontal dashed lines indicate no recovery. Error bars are 95% CI of the mean. For details on the recovery rates, see Materials and Methods.

Discussion

Our results show that a first fire event in floodplain forests completely destroys the trees, and over 90% of the superficial root system and tree seed bank, favoring the invasion of herbaceous vegetation. Yet, these forests slowly recover their structure and species richness, with recruiting trees precluding the growth of herbaceous plants (Fig. 3.4 b). However, if a second fire event occurs within a few decades, as we have seen in 48% of the fire scars of the middle Negro region, forest recovery rates drop and herbaceous cover persists. In these twice burnt sites, trees that recruit seem to co-exist with high herbaceous cover (Fig. 3.4 c), revealing a strategy often used by savannas trees (Sankaran, Ratnam & Hanan 2004; Silva *et al*. 2013; Staal & Flores 2015). In tropical upland savannas, high herbaceous cover limits the recruitment of forest trees by resource competition and by spreading fires, which favors dominance of savanna trees (Hoffmann et al. 2004; Bond 2008). Future research should unravel if comparable mechanisms are taking place in repeatedly burnt floodplains.

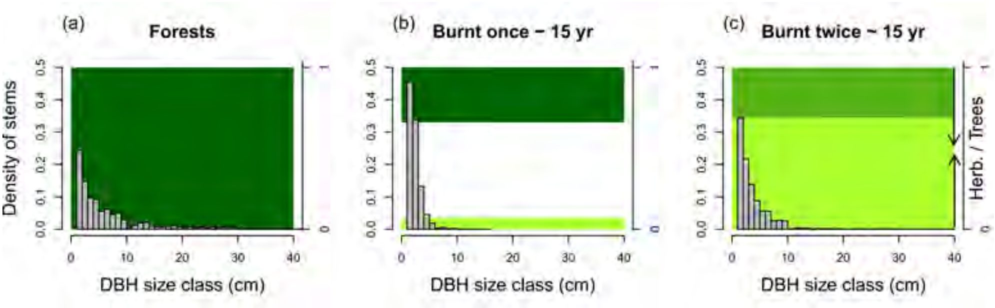

Figure 3.4. Tree recruitment vs. invasion of herbaceous vegetation.(a) unburnt forests; (b) burnt forests 15 years after one fire; (c) old burnt forests ~ 15 years after second fire (~ 30 years after the first, see Table 3.1). Histograms are stem density by DBH class, based on three replicate plots. Dark green background fills from top to bottom, showing tree basal area as a fraction of the basal area in unburnt forests. Light green background fills from bottom to top and shows ground cover by herbaceous plants. Note that trees and herbaceous plants co-exist in twice burnt sites (c), but not in once burnt sites (b) with similar tree basal area.

Forests in blackwater ecosystems seem to recover remarkably slower than in most uplands after fire. Upland forests usually recover closed canopies even after several fire events, despite changes in tree composition (Mesquita *et al.* 2001; Gehring, Denich & Vlek 2005; Barlow & Peres 2008; Vargas, Allen & Allen 2008; Jakovac *et al.* 2015). In uplands abandoned after several cycles of slash-and-burn agriculture, secondary forests attain a tree basal area of 10-37 m^2/ha and tree species richness of 25 - 60 species after 15 years (Saldarriaga *et al.* 1988, Brown & Lugo 1990, Guariguata & Ostertag 2001,Williamson *et al.* 2014). Instead we found that blackwater floodplains, even when burnt only once, recover tree basal area and species richness at rates that are amongst the lowest of tropical ecosystems (10 m^2/ha and 15 species after 15 years).

Upland forests in the Amazon lose 50 - 98% of their seed banks to fire (Nepstad *et al.* 1996, Kennard *et al.* 2002), but recover when survival or recruiting trees attract animal dispersers that replenish the seed bank (Young, Ewel & Brown 1987; Nepstad *et al.* 1996). In burnt floodplain forests, both the trees and seed banks were completely destroyed. Because most seeds in these forests are dispersed by water, fish, and terrestrial animals attracted by the forest canopy (Kubitzki & Ziburski 1994), the high tree mortality and slow recovery we found may limit the dispersal of tree seeds to burnt sites. For instance, Ritter, Andretti & Nelson (2012) found that burnt blackwater forests did not recover and had bird communities similar to those of savannas for more than 25 years after fire. This suggests that changes in seed dispersal may contribute to limit forest regeneration for a long time.

In synthesis, our results show that two fire events can undermine the recovery capacity of blackwater forests. After a first fire, forests can still recover. Yet, after a second fire, a non-forest state persists and recruiting trees seem to fail suppressing herbaceous plants. Also in temperate wetlands, fire can trigger shifts from forest to persistent treeless vegetation (Fletcher, Wood & Haberle 2014). Trees in both tropical and temporal floodplain forests are strongly limited by nutrient availability and waterlogging (Junk et al. 2011) undermining the capacity of forests to recover from repeated fire perturbations. Comparable patterns of arrested succession after recurrent fires have been observed in dry Mediterranean ecosystems where regrowth of trees and shrubs is strongly limited by summer droughts (Acácio *et al.* 2007). Our results suggest that in tropical floodplains, forest recovery after fire may be limited by low resource availability, lack of tree seeds and competition with herbaceous vegetation.

Managing the impact of fire regimes

Avoiding the use of fire in tropical forests during drought is challenging, yet an effective management strategy for conservation (Barlow and Peres 2004, Aragão & Shimabukuro 2010, Barlow *et al.* 2012). Dry episodes, like those associated with El Niño Southern Oscillation (ENSO), increase fire severity (Chen *et al.* 2011) and reduce tree cover across the wet tropics (Holmgren *et al.* 2001; 2013). As ENSO droughts become more frequent (Cai, Borlace & Lengaigne 2014), the expansion of fire-prone vegetation may have serious implications. For instance, greenhouse gas emissions may increase due to the release of carbon to the atmosphere from burning forest biomass and peat deposits (Lähteenoja, Flores & Nelson 2013; Grace, Mitchard & Gloor2014). Therefore, fire prevention in blackwater forests during drought events may be the most practical way to protect this ecosystems' unique biodiversity as well as its capacity to provide resources for local peoples.

Acknowledgements

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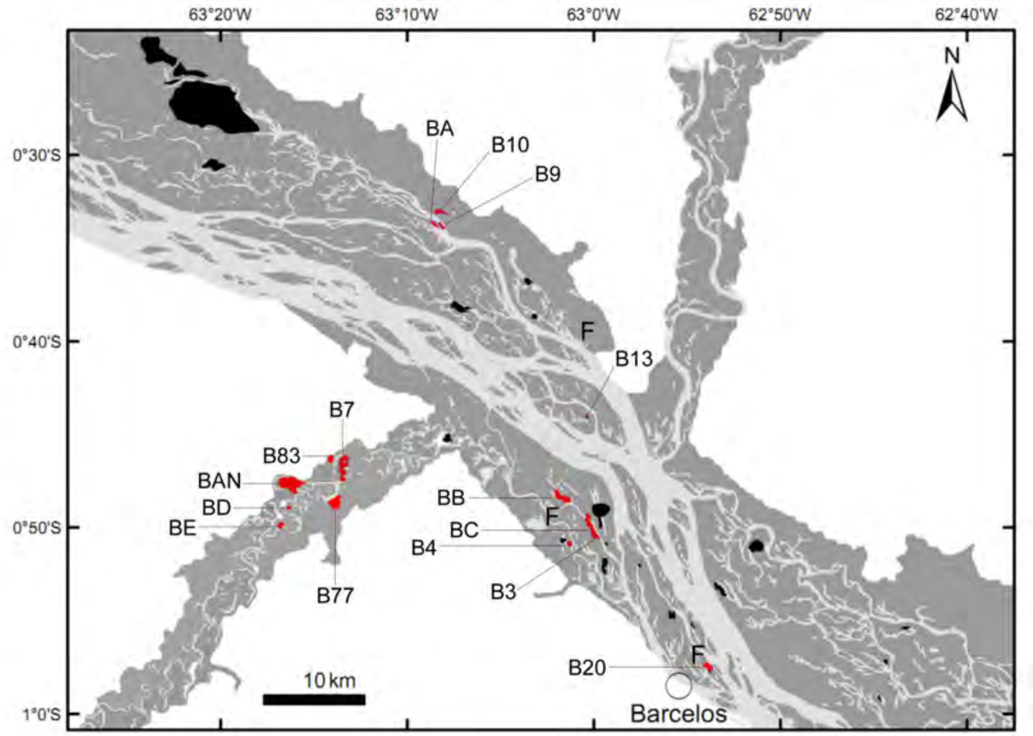
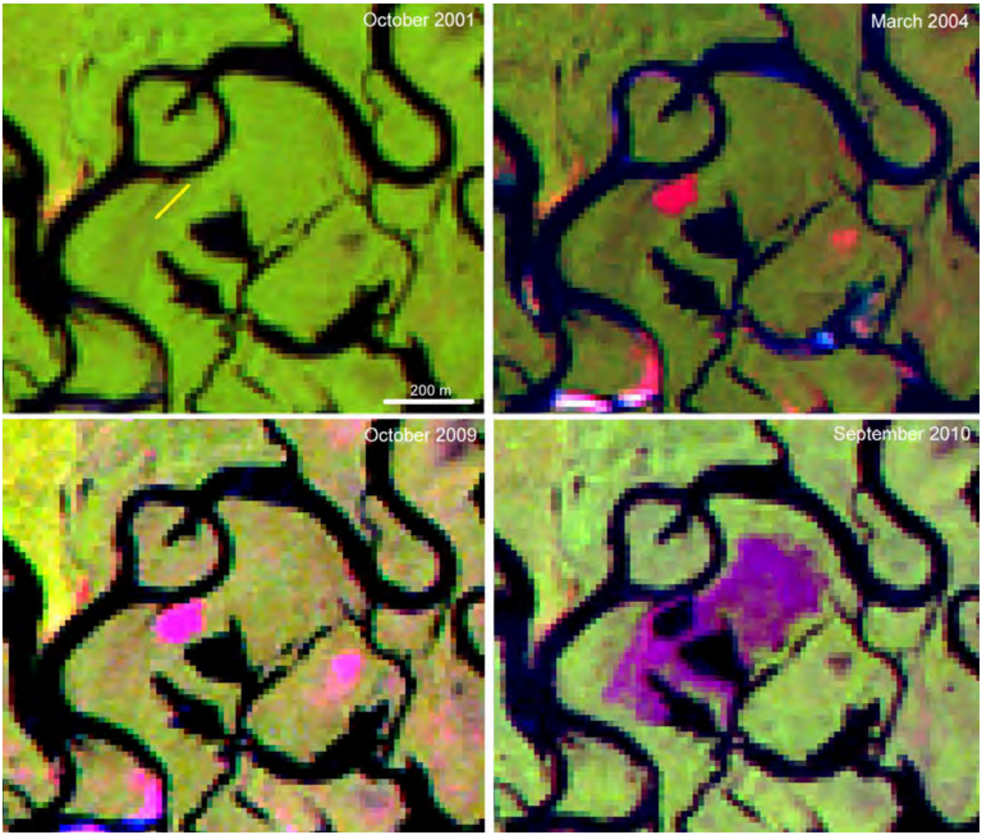
Appendices



Appendix 3.1. Map of study area showing the location of all field plots that we analyzed, including burnt sites (first letter B) and unburnt forest reference plots (letter F). More information in Table 3.1 of main text.

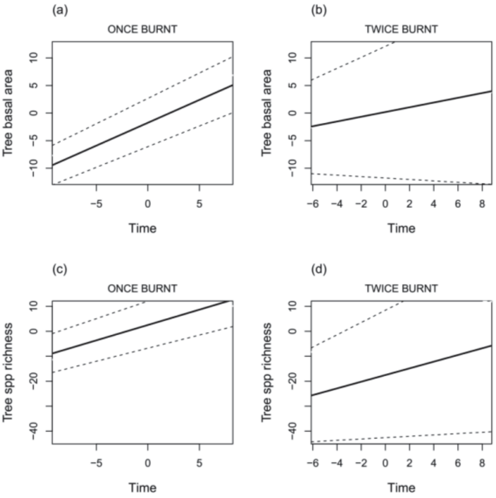
Appendix 3.2. Example 1 of the use of Landsat TM images to identify fire dates, along the lower Cuiuini River, a tributary of the Negro River. A first fire occurred in the dry season of 1997-1998, removing most of the forest canopy. The second fire occurred in the early months of 2004 and was inferred from the expansion of the old fire scar´s borders. The yellow line shows the approximate location of our plot. Both fires occurred in extreme droughts shown in Fig. 3.1.



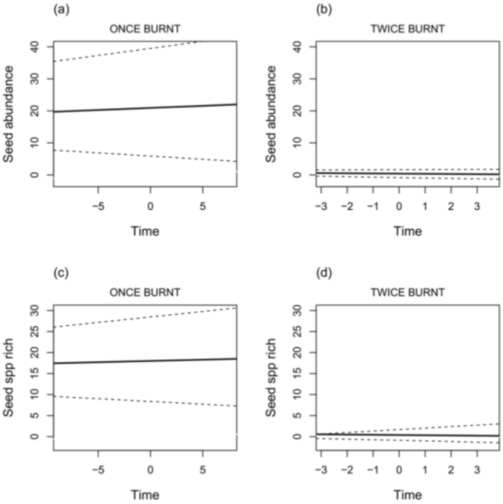
Appendix 3.3. Example 2 of the use of Landsat TM images to identify fire dates in the lower Cuiuini River. The first fire occurred in the beginning of 2003 (low water season), removing the forest canopy over ~ 2 ha. The second fire occurred in the early months of 2010, expanding the borders of the fire scar. The yellow line shows the approximate location of our plot. Both fires occurred in extreme droughts shown in Fig. 3.1.

Appendix 3.4. Statistical results from multiple linear regressions. Each response variable was analyzed as a function of “time after last fire” and “dry phase length”.

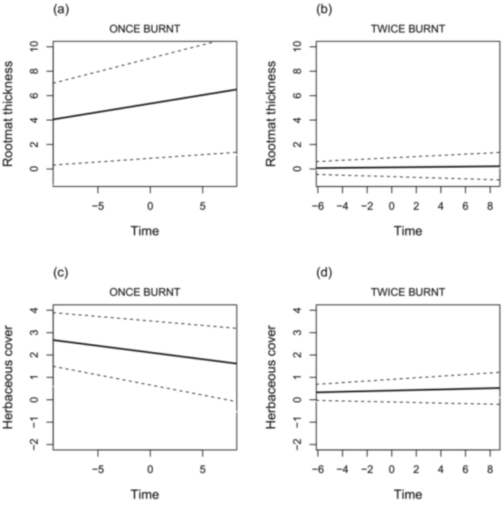
Response variable	**Number of fires**	**Time (slope)**	**Time (p value)**	**Dry phase (slope)**	**Dry phase (p value)**
Tree basal area	1	0.83	**0.001**	-0.005	0.83
Tree basal area	2	0.43	0.27	0.003	0.93
Tree spp. richness	1	1.23	**0.003**	-0.04	0.43
Tree spp. richness	2	1.35	0.11	0.12	0.13
Seed abundance	1	0.13	0.62	-0.12	0.22
Seed abundance	2	-0.05	0.48	0.001	0.89
Seed spp. richness	1	0.07	0.67	-0.1	0.11
Seed spp. richness	2	-0.05	0.48	0.001	0.89
Rootmat thickness	1	0.14	**0.08**	-0.03	0.16
Rootmat thickness	2	0.01	0.68	0.0002	0.91
Herbaceous cover	1	-0.06	**0.05**	-0.01	0.33
Herbaceous cover	2	0.01	0.44	0.002	0.14



Appendix 3.5. Effect of time on the recovery of trees, used to produce Fig. 3.3. Each graph shows the mean slope and its 95 % confidence interval (produced by bootstrapping) for the partial effect of "time after the last fire", from multiple regressions where the independent variables are "time after last fire" and "length of dry phase".



Appendix 3.6. Effect of time on the recovery of tree seed bank, used to produce Fig. 3.3. Each graph shows the partial effect of “time after last fire” from multiple regressions, as in Appendix 3.5.



Appendix 3.7. Effect of time on the recovery of the root mat thickness and on the change in herbaceous cover, used to produce Fig. 3. Each graph shows the partial effect of “time after last fire” from multiple regressions, as in Appendix 3.5.

Chapter 4

Savannization of Amazonian floodplain forests

Bernardo M. Flores and Milena Holmgren

Abstract

Tropical forests in many parts of the world are expected to shift into a savanna state as drought and fire events accentuate with global warming. Studies of current savanna-forest transitions typically find that fire exclusion results in forest expansion and soil fertilization. It seems reasonable to imagine that the transition in the opposite direction, from forests to savannas, may involve fires, soil degradation and the invasion of savanna trees. Surprisingly, this process has never been empirically demonstrated. Here we show that in seasonally inundated forests of the Amazon, a first fire triggers the loss of soil fertility which intensifies in subsequent years while savanna trees become dominant. This savannization of burnt forests occurs in a timeframe of less than four decades, possibly accelerated by strong soil erosion from annual floods. The new ecosystem state is characterized by poor sandy soils and savanna trees. Our findings support the idea that plant-soil-fire interactions may drive forest savannization, and reveal that savannas can expand from unsuspected places.

Significance

Climate change may favour the expansion of savannas in tropical regions, altering biome distribution with consequences for biodiversity and ecosystem services. Here we show evidence of savannization in the Amazon forest. Fires and soil degradation mediate a tree compositional shift, possibly accelerated by intense nutrient leaching and soil erosion. This insight can help explain why most tropical forests persist in the face of fires, and suggests that under chronic perturbation, soil erosion may gradually undermine forest resilience.

Massive fires penetrated deep into tropical forests in the Amazon (Aragão et al. 2007; Alencar et al. 2015), and Indonesia (Page et al. 2002) during recent drought events, heating the debate of whether these forests could persist in a drier future. In the past thousands of years, forest-savanna transitions were associated to drier climates and fires (Mayle and Power 2008). Normally, the closed canopy of tropical forests precludes grass growth, suppressing fire spread (Archibald et al. 2009; Murphy and Bowman 2012). During drought, however, fires can percolate more easily through forested landscapes (Page et al. 2002; Aragão et al. 2007; Alencar et al. 2015; Pueyo et al. 2010; Flores et al. 2014) opening the understory for new fires

(Cochrane et al. 1999). It is hypothesized that under recurrent fire, the ecosystem can be trapped in an open vegetation state (Grady and Hoffmann 2012), allowing the expansion of fire-prone vegetation (Archibald et al. 2009; Murphy and Bowman 2012; Hirota et al. 2010; Hoffmann et al. 2012; Staal and Flores 2015; Dantas et al. 2016).

The contrasting strategies of forest and savanna trees to suppress or promote flammability (Bond and Midgley 1995; Sankaran et al. 2004; Silva et al. 2013) in part contribute to stabilize sharp vegetation boundaries in ecotonal regions (Hirota et al. 2011; Staver et al. 2011; Gray and Bond 2015; Staal and Flores 2015). This bistability has been observed in the analyses of satellite tree cover (Hirota et al. 2011; Staver et al. 2011) and field tree cover data from across the tropics (Staal and Flores 2015), yet it can also change as a function of climate (Hirota et al. 2010; Staal et al. 2016). It has been shown that where annual rainfall is below ~1700 mm in South America, savannas are more stable than forests, and therefore more likely to expand (Staal et al. 2016). In tropical landscapes, yet particularly in South America, savannas have relatively less fertile and sandier soils, compared to forests (Jackson 1968; Bond 2010; Veldman and Putz 2011; Wood and Bowman 2012; Dantas et al. 2013; Lehmann et al. 2014; Gray and Bond 2015; Paiva et al. 2015; Veenendaal et al. 2015; Pellegrini 2016). Savanna and forest tree communities are also formed by different species, with contrasting adaptations to fire, and to resource availability such as root biomass (Hoffmann et al. 2003; Hoffmann et al. 2009; Silva et al. 2013; Dantas et al. 2016). Therefore, it seems reasonable to expect that savanna expansion implies on the loss of soil fertility, the expansion of savanna trees, and of flammability across the landscape. For instance, forest tree encroachment in Neotropical and African savannas leads to soil fertilization (Moreira 2000; Coetsee et al. 2010; Silva et al. 2013; Pellegrini et al. 2014; Pellegrini et al. 2015). This same pattern of soil fertilization was found when forests expanded over savannas in the past (Silva et al. 2008; Silva and Anand 2011). Evidence of current savanna expansion over tropical forests, however, is very limited. The best documented cases of savannization were the result of centuries of intensive land-use, fire and cattle ranching leading to soil erosion and the replacement of upland tropical forests by true savanna vegetation (Borhidi 1988; Cavelier et al. 1998). More often, tropical forests tend to recover canopy closure fast after small-scale perturbations (Jakovac et al. 2015; Devisscher et al. 2016; Poorter et al. 2016), revealing that the transition to savanna does not occur so easily (Barlow and Peres 2008; Veldman and Putz 2011).

The capacity of forests to persist after fire may depend on several factors such as fire severity and scale, adaptations of the tree community to fire, the capacity of trees to disperse into burnt sites, and to overcome local environmental filters. Simple models of vegetation dynamics based on the plant-fire feedback usually consider that low resource environments are more likely to be found in the savanna state and high resource environments in the forest state. The reason is that resource availability determines forest recovery rate and hence the chance of being trapped by fire (Grady and Hoffmann 2012; Hoffmann et al. 2012; Murphy and Bowman 2012). An alternative view is that soils can change and be changed by plants and fire, in a plant-soil-fire feedback mechanism that can drive biome transitions (Silva et al. 2013; Staal and Flores 2015; Jackson 1968; Bond 2010; Wood and Bowman 2012; Paiva et al. 2015; Pellegrini 2016). Forest tree species contribute to enrich the soil with high quality litter (Paiva et al. 2015), which favours the recruitment of forest trees with higher nutrient demands (Bond 2010; Hoffmann et al. 2012; Paiva et al. 2015; Pellegrini 2016). This positive feedback may also apply to savannas, where lower quality litter produced by savanna trees maintains poorer soils and favours savanna tree recruitment (Paiva et al. 2015). It has also been shown that after fire, soils can be eroded by water runoff during heavy rain events, losing its fertility (Prosser and Williams 1998; Shakesby and Doerr 2006). Therefore, when fire penetrates a rainforest, it's recovery rate implies not only in escaping from a 'fire trap' (Grady and Hoffmann 2012), but also from a 'soil degradation trap' (Prosser and Williams 1998; Shakesby and Doerr 2006). A fast recovery of the forest structure allows also the recovery of soil fertility (Davidson et al. 2007). Yet when forests persist open for a long time (Flores et al. 2016), soils may degrade more severely.

Here we investigate this alternative mechanism by assessing forest savannization at the core of the Amazon Basin. Our study area is an extensive floodplain landscape that hosts mostly forest, but also islands of savanna (Appendix 4.1). Fires can percolate through these floodplain forests in dry years with a severe impact (Flores et al. 2014; Flores et al. 2016). Because of seasonal inundation, we expect that post-fire soil erosion is higher, compared to other forest ecosystems (Shakesby and Doerr 2006). We hypothesized that after fire, soils of floodplain forests would degrade, and savanna trees would become dominant in a savannization process. Using Landsat images, we mapped 40 years (1973-2012) of forest fire history, identifying 27 fire scars (Appendix 4.1), of which 13 (48%) were burnt twice. We selected 15 burnt forests to produce a (space-for-time) chronosequence, which we used to analyze changes in tree composition, and several soil properties up to 36 years after the first fire. We selected three mature forests and three savannas from the same landscape, as reference for the alternative states in the vegetation (see Appendices 4.2 and 4.3).

Results and discussion

Soil degradation after fire

Despite short increases in the concentration of some nutrients immediately (3 years) after the first fire, we found that most nutrients and also clay fraction decrease, while sand fraction increases with time (Fig. 4.1). Soil changes continue for 36 years in a linear trend towards the levels found in savannas. As in other tropical ecotones (Jackson 1968; Bond 2010; Veldman and Putz 2011; Wood and Bowman 2012; Dantas et al. 2013; Lehmann et al. 2014; Gray and Bond 2015; Paiva et al. 2015; Veenendaal et al. 2015; Pellegrini 2016), we found that soils of mature forests are richer in nutrients and clay, compared to savanna soils. Our chronosequence revealed that a first forest fire is the onset of a forest-savanna soil transition. In different ecosystems across the world, leaching of soluble nutrients and soil erosion is common following wildfire (Lewis 1974; Prosser and Williams 1998; Thomas et al. 1999; DeBano 2000; Gimeno-Garcia et al. 2000; Certini 2005; Murphy et al. 2006; Shakesby and Doerr 2006). The destruction of forest structure and litter cover by fire is known to alter particle size distribution by allowing the erosion of finer soil fractions (Thomas et al. 1999; Certini 2005; Shakesby and Doerr 2006). Indeed, we found that after a first fire, clay decreases and sand increases consistently (Fig. 4.1 a,b). To explain this soil shift from clayey to sandy, we thought of two possible mechanisms. In the burnt sites with open vegetation (Flores et al. 2016), water currents and turbulence can erode fine clay sediments, and also deposit sand from the river water (Latrubesse and Franzinelli 2005).

In upland Amazonian forests, soil fertility normally recovers during secondary succession following the abandonment of land-use with fire (Davidson et al. 2007). In addition, the fast recovery of upland forest biomass (Poorter et al. 2016) reduces the phase in which the soils are more vulnerable to erosion (Prosser and Williams 1998). In uplands, soils may erode more intensely during heavy rain events after fire (Shakesby and Doerr 2006). This happens because severe fires may increase soil water-repellency leading to higher runoff (DeBano 2000). Also, the loss of forest litter cover to fire lowers the soil's resistance to erosion (Prosser and Williams 1998). These mechanisms may be especially important in hilly terrains (Cavelier et al. 1998), where soils need to resist intense runoff conditions. However, when forests recover as slow as in these floodplains (Flores et al. 2014; Flores et al. 2016), erosion and leaching may continue washing soil nutrients out of the system for a long time. In blackwater floodplain forests, trees commonly form a thick root-mat filled with humus (dos Santos and Nelson 2013), which can be associated with ectomicorriza (Singer and Aguiar 1986), facilitating nutrient retention and recycling (Stark and Jordan 1978). Yet in dry years (Flores et al. 2014), fires can destroy the forest root-mat layer (Flores et al. 2016), which may lower the soils' resistance to erosion during seasonal inundation.

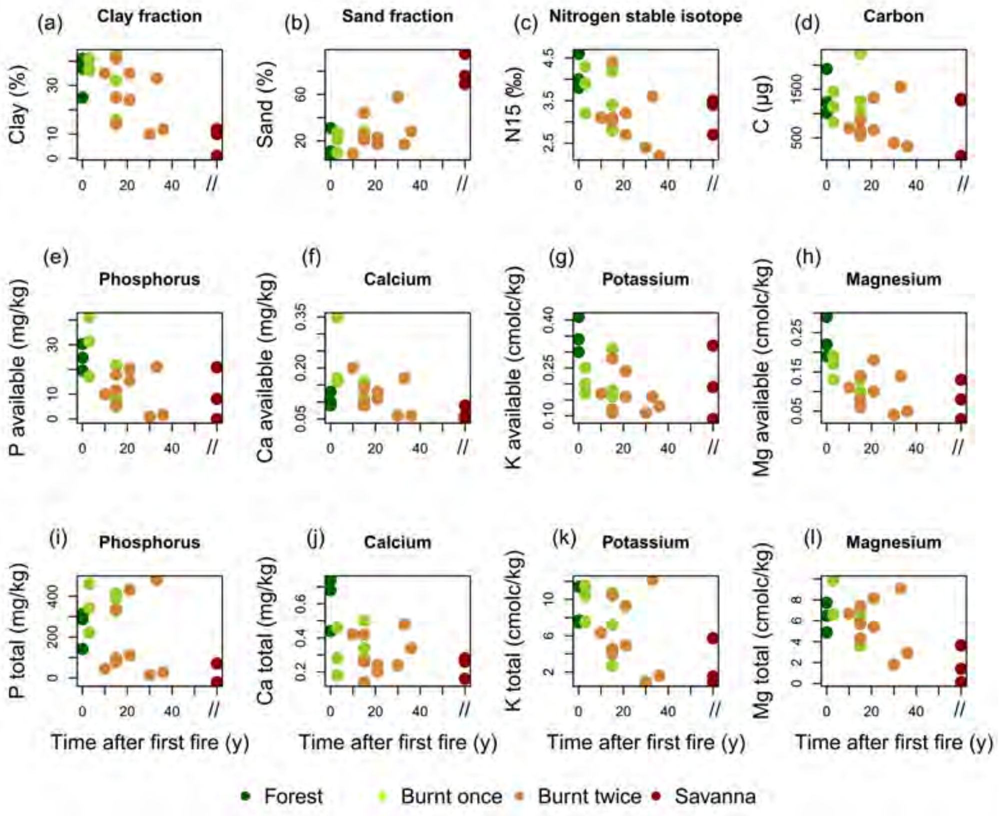


Figure 4.1. Soil degradation with time after fire in floodplain forests. Different treatments reveal that after each fire event, soils continue degrading with time, suggesting the existence of a leaching mechanism besides fire. See Appendix 4.3 for details.

In summary, our results show that fire in Amazonian blackwater forests may trigger a long-term loss of nutrient and clay, making soils similar to savanna soils (Fig. 4.1; Appendix 4.4). Such drastic soil degradation is expected to have consequences for tree recruitment due to environmental filtering. While soil conditions become increasingly harsh for forest trees, such conditions may select for plant species that are more adapted (Bond 2010; Hoffmann et al. 2012; Paiva et al. 2015; Pellegrini 2016). Compared to forest trees, savanna trees have well developed roots (Canadell et al. 1996; Jackson et al. 1996; Hoffmann et al. 2003), which help obtaining nutrients when soil fertility is low.

Tree compositional shift

We found that tree composition shifts along the chronosequence that starts with a first forest fire. Our analyses of ordination of the tree community, in which the distance between field plots reflects their species similarity based on most abundant trees, clearly separated forests and savannas along the second axis (Appendix 4.5 a). The 'tree community ordination axis 1' was related to the 'dry phase length' (Fig. 4.2 a). This finding supports previous studies that find floodplain tree species distributed along topographic zones (Wittmann et al. 2006; Wittmann et al. 2010). The 'tree community ordination axis 2' was related to 'time after first fire' (Fig. 4.2 b), and 'number of fires' (Fig. 4.2 c), with forests and savannas on the extremes and burnt sites in between (see also Appendix 4.6). Composition of the tree community is initially dominated by forest tree species, yet with time and the occurrence of a second fire event, the community becomes strikingly dominated by savanna species. This result implies that fire disturbance may contribute to structure floodplain tree community, together with inundation.

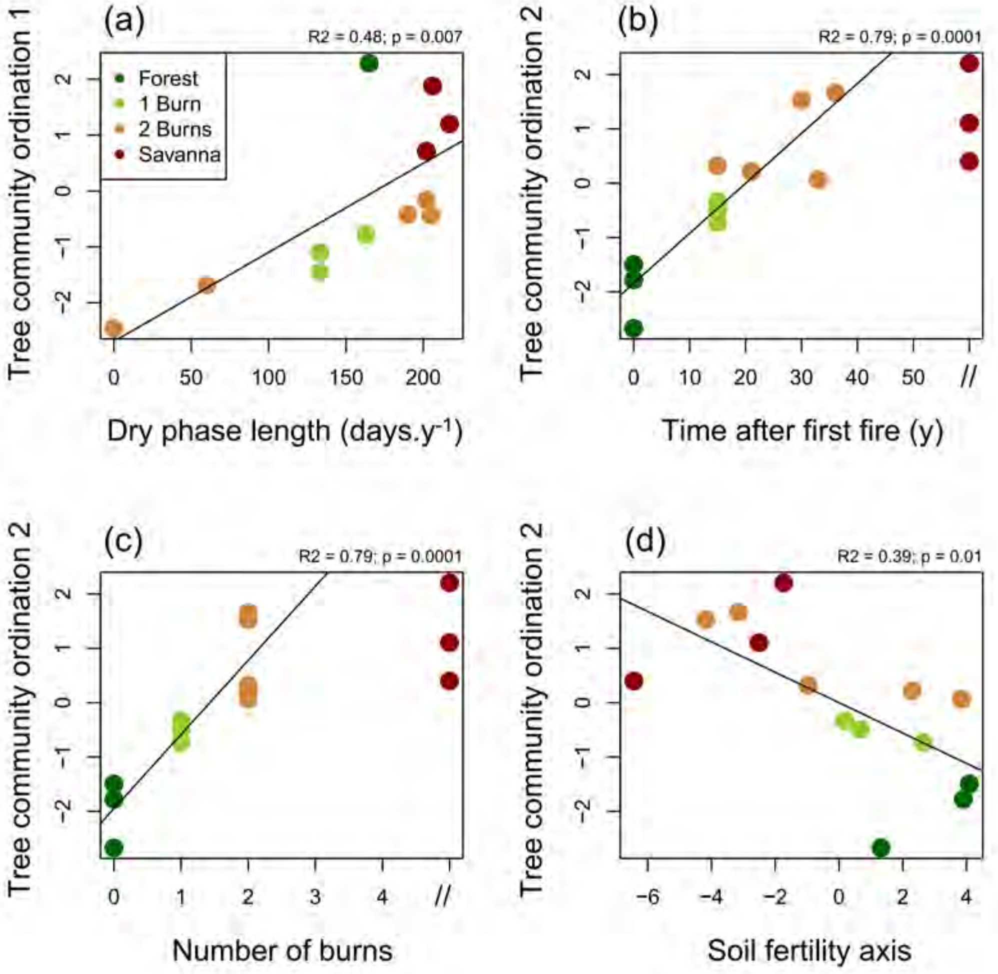


Figure 4.2. Tree community ordination axes vs. inundation, fire and soil. (a) 1st ordination axis vs. dry phase length; (b) 2nd ordination axis vs. time after first fire, (c) 2nd ordination axis vs. number of burns, and (d) 2nd ordination axis vs. the soil fertility axis (PCA axis 1 in Appendix 4.4 b). See Appendix 4.3 for details. Regression lines for (b) and (c) do not include savannas.

Our principal component analysis (PCA) of the soil captured the variation of several soil variables along different axes, with most of the fertility gradient of floodplain soils represented by the first axis (Appendix 4.5 b). As predicted, this 'soil fertility axis' was significantly related to the 'tree community ordination axis 2' that represented forest-savanna transition (Fig. 4.2 d). A similar pattern was found for most soil variables alone in relation to the 'tree community ordination axis 2' (Appendix 4.7). These results show that a first fire is the onset of forest savannization in these ecosystems. The simultaneous loss of soil fertility and forest tree species may imply that this transition is accelerated by the positive feedback between soil and trees (Paiva et al. 2015).

The combined analyses of two ecosystem dimensions: the soil and the tree community composition, revealed how a fire may trigger forest-savanna transition (Fig. 4.3). Most studies on tropical vegetation dynamics have shown evidence that forests and savannas can be alternative stable states, maintained by the interplay of fire, tree adaptations, and resources such as rainfall and soil fertility (Hoffmann et al. 2003; Hoffmann et al. 2009; Silva et al. 2013; van Nes et al. 2014; Dantas et al. 2016). Transitions between biomes had only been assessed with palaeoecology (Mayle and Power 2008), or during forest encroachment in savannas protected from fire (Moreira 2000; Coetsee et al. 2010; Pellegrini et al. 2014; Pellegrini et al. 2015). In addition to the long-term forest savannization shown in Colombia (Cavelier et al. 1998), this may be the first study ever to demonstrate forest-savanna transition using a known landscape fire history (Appendices 4.1 and 4.2). The patterns we found, in which fertile clayey forests shift into nutrient poor sandy savannas, may also be an indication of how sandy savanna islands across the Amazon were formed, considering that many are palaeo floodplains (Rossetti et al. 2012).

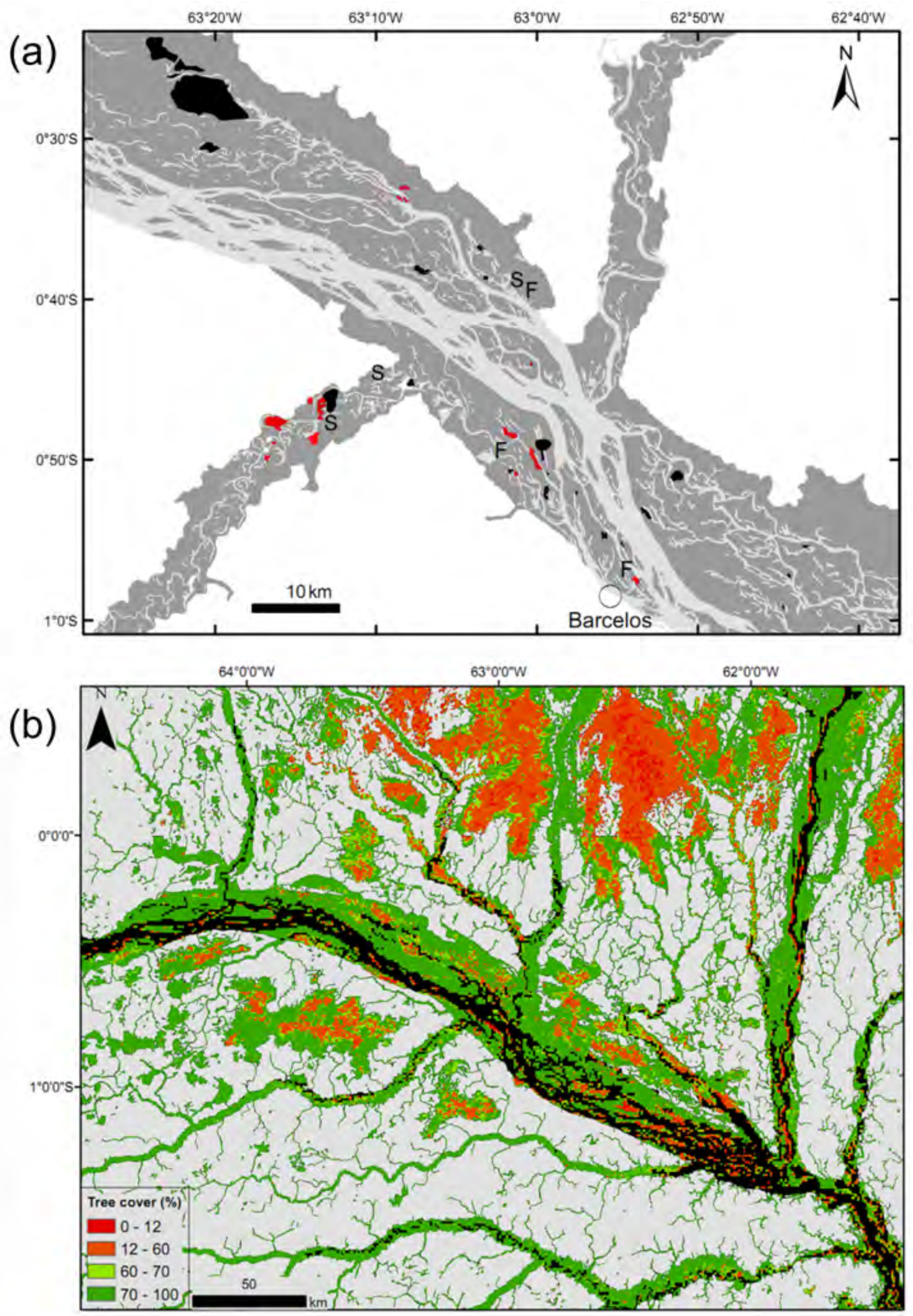
Figure 4.3. Mechanisms that can mediate forest-savanna transition. Fires export nutrients stored in the forest trees and soil, and favour further nutrient leaching while tree cover remains open. Degraded soils will limit the recruitment of forest tree species, but not of savanna trees that dominate, co-existing with flammable herbaceous vegetation. Photos of Negro river floodplains by B. M. Flores.

The impact of fire on tropical forest resilience is a major issue in environmental science, yet the existence of few evidence on the role of fire for forest savannization has lowered the confidence on this mechanism (IPCC 2014). An important detail is that once a fire penetrates into tropical forests, flammability increases (Cochrane et al. 1999). Nonetheless, despite recent intensification of the fire regime and fire severity in transitional Amazonian forests (Brando et al. 2014; Alencar et al. 2015), the invasion of native and exotic grass vegetation was shown to be limited (Silvério et al. 2013; Brando et al. 2014). Other studies refute the interpretation of savannization, arguing that most Amazonian forests actually remain in a degraded forest state (Barlow and Peres 2008; Veldman and Putz 2011). Here, we show with field data on several soil properties and tree composition that fire can destabilize tropical forests, allowing the expansion of true savanna vegetation. Our findings support the idea that plant-soil-fire interactions may accelerate savanna expansion as extreme climatic events intensify (Franco et al. 2014). Savanna expansion in floodplains may even be contagious to uplands, as both ecosystems share more than 30% of local tree species (Terborgh and Andresen 1998; Wittmann et al. 2006). Therefore, the prediction that extreme climatic events will become more frequent (IPCC 2014) implies that fires will burn more often (Chen et al. 2011), and spread the risk of savannization throughout the Amazon.

Methods

We produced a chronosequence (space-for-time) using burnt forests with different 'time after first fire' ranging from 3 to 36 years, and selected intact forests and savannas as reference for both biomes in the same landscape. Fires were identified with Landsat images (see Appendix 4.1 a). In a total of 21 plots with 0.6 ha (Appendix 4.3), we collected superficial (0 - 20 cm) compound soil samples for the analysis of several soil variables and identified all trees above 1 cm in DBH. More detailed methods in Appendix 4.2.

Appendices



Appendix 4.1. Floodplain landscape at the Negro river, Central Amazon. (a) in black: forests burnt in past ~ 40 years (see Appendix 4.2 for details), in red: fire scars we studied; (b) distribution of forests and savannas based on tree cover data (DiMiceli et al. 2011) across floodplains separated by Wetlands' mask (Hess et al. 2015), in gray: upland or *terra-firme*, rectangle: shows (a)

Appendix 4.2. Detailed methods.

Sampling design. We studied floodplains at the middle Negro river and tributaries (Fig. S1), Central Amazon. One-seventh of the Amazon is floodable, and approximately half of this area has strong influence of black water rivers (Hess et al. 2015). Despite the naturally low nutrient availability of these floodplains, forests can attain high biomass (Terborgh and Andresen 1998). Using Landsat images for 1973-2012, we identified several forest fires, of which we selected 15 based on the number of times they had been burned and the time passed since the first burn (Appendix 4.3). Three mature forests and three savannas were chosen in the same landscape as reference (Appendix 4.1). We identified the first fire when the forest canopy was transformed into open water during high water months and bare soil during low water months. The second fire was identified either when the old burn scar expanded (which we assumed re-burning), or when regenerating vegetation returned to bare soil (for more details see Flores et al. 2016). In all 21 sites we established plots of 0.6 ha (150 x 40 m), placed at least 30 m from the borders, and at least 100 m from river channels, to measure tree floristic composition and several soil variables.

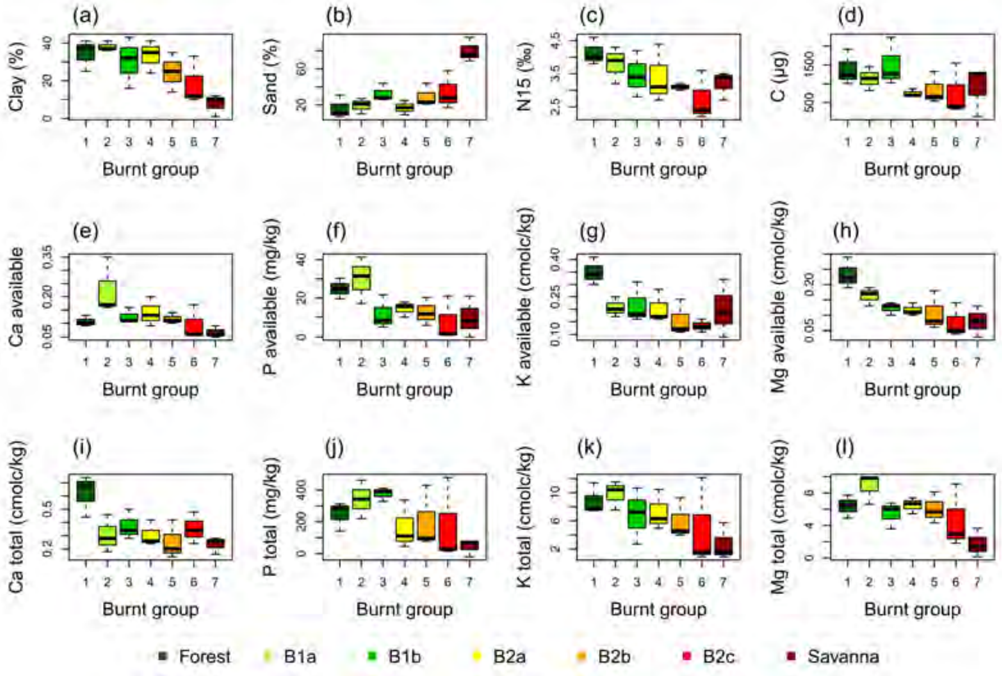
Vegetation data. Along 150 m of each plot's centerline, we identified small trees (1-10 cm in diameter at breast height - DBH) within 2 m of width, medium trees (10-30 cm in DBH) within 20 m, and large trees (>30 cm in DBH) within 40 m. All tree species found for the first time in each plot were collected, and brought to Manaus to be first identified by a para-botanist with the help of photos of the trunk and other structures such as roots, and later compared with photos from herbariums.

Soil data. Along 150 m of each plot's centerline, we collected superficial soil (0 - 20 cm) including the organic layer, at three evenly spaced positions to produce a compound sample. Collected soils were brought to Manaus to be analyzed in the Plant and Soil Laboratory (LTSP) of the National Institute for Amazonian Research (INPA). A technician analyzed mineral fractions, available and total nutrients. The nitrogen stable isotope (15N) analysis was carried out at the Stable Isotope Facility of the University of California (UCDavis), USA. All analyzes were done using standard procedures.

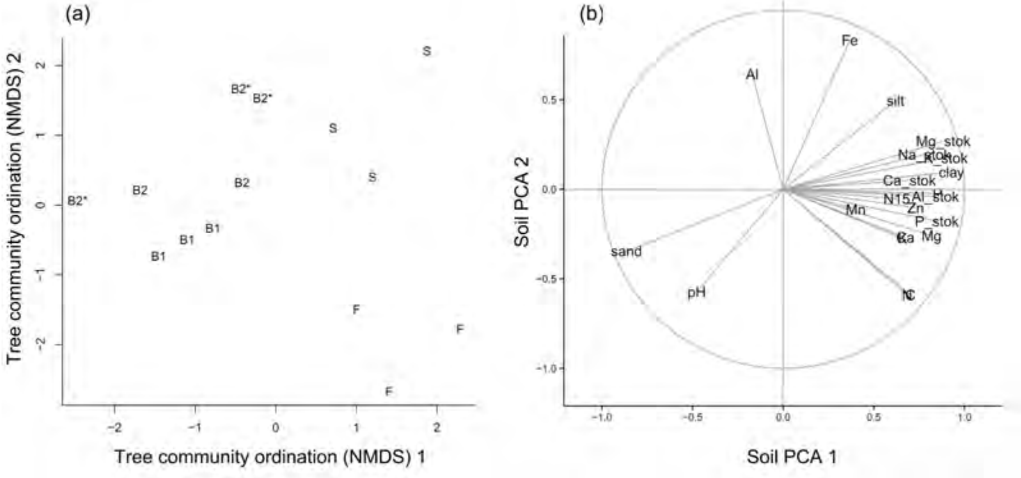
Dry phase length. Dry phase length per plot was estimated for each site from three measurements of the water column depth, on a known date in the high water season. The depth was compared to the water level at the station on the same day to calculate the average number of days per year each plot stayed above water. Historical water level data for Barcelos station (1968 - present) was obtained from the *Agência Nacional de Águas* (http://hidroweb.ana.gov.br/).

Appendix 4.3. Plots used in this study and available data. All plots were sampled in 2013.

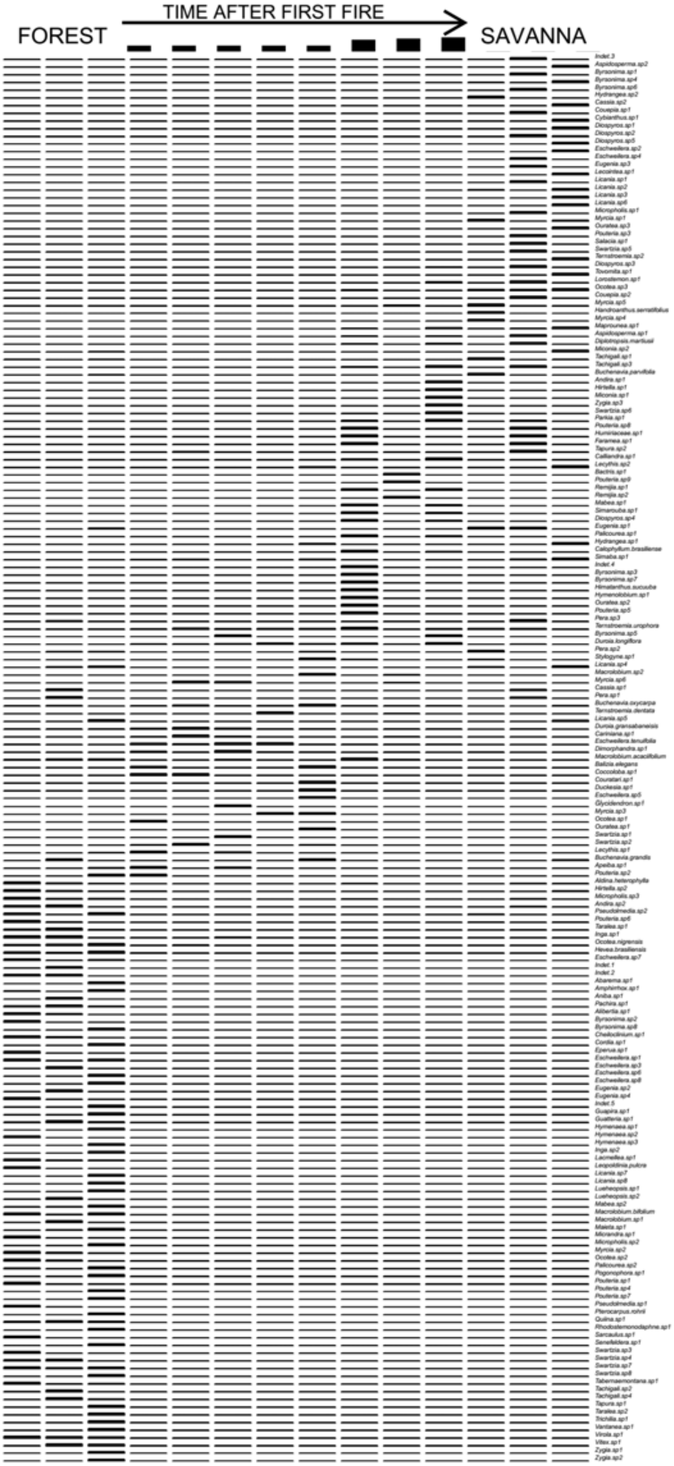
Site	# of fires	Fire dates	Dry phase (days.y^{-1})	Soil data	Tree composition data
Forest 1	0	•	•	Yes	Yes
Forest 2	0	•	•	Yes	Yes
Forest 3	0	•	165	Yes	Yes
BA	1	2010	130	Yes	No
BB	1	2010	172	Yes	No
BC	1	2010	172	Yes	No
B9	1	1998	133	Yes	Yes
B10	1	1998	163	Yes	Yes
B13	1	1998	133	Yes	Yes
B3	2	1998 / 2010	180	Yes	No
BD	2	2003 / 2010	165	Yes	No
E	2	1992 / 2010	172	Yes	No
B4	2	1998 / 2004	60	Yes	Yes
B7	2	1998 / 2004	190	Yes	Yes
BAN	2	1998 / 2004	197	Yes	No
B20	2	1980 / 1992	30	Yes	Yes
B83	2	1983 / 2004	202	Yes	Yes
B77	2	1977 / 1998	205	Yes	Yes
Savanna 1	Unknown	Unknown	206	Yes	Yes
Savanna 2	Unknown	Unknown	202	Yes	Yes
Savanna 3	Unknown	Unknown	217	Yes	Yes



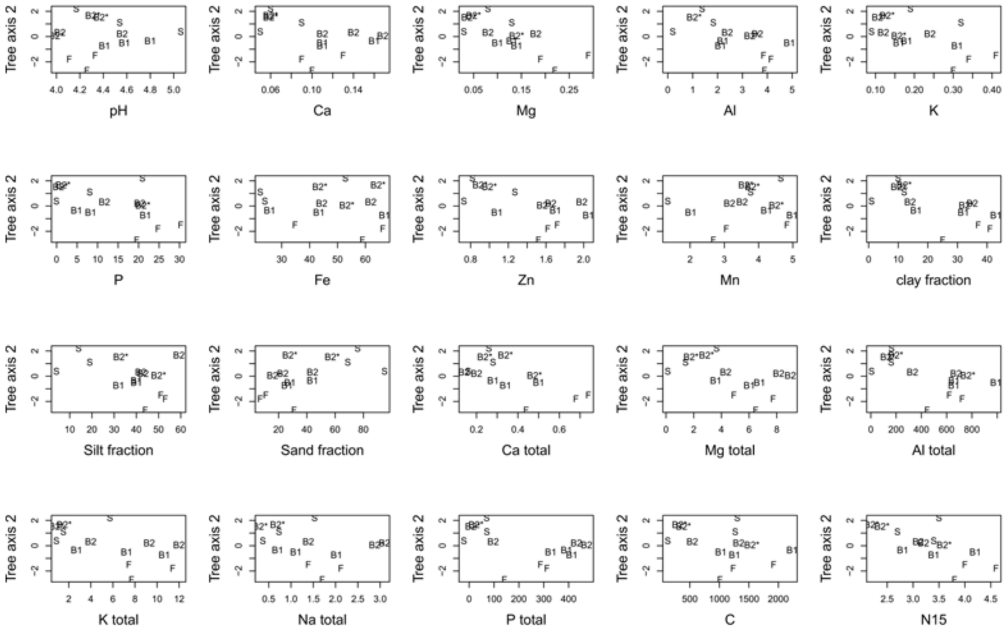
Appendix 4.4. Change in soil properties with number of fires and time after fire (in groups), showing that soil degradation continues after each fire. Groups: 1 – forests; 2 – burnt once three years before; 3 – burnt once 15 years before; 4 – burnt twice three years before; 5 – burnt twice nine years before; 6 – burnt twice ~15 years before; and 7 – savannas. See Appendix 4.2 for information on treatments.



Appendix 4.5. Structures of (a) tree community and (b) soil components of the floodplain ecosystem. Letters in (a) indicate groups: F – forests; B1 – burnt once; B2 – burnt twice; B2* – old burnt twice; and S – savannas. First and second axes explained most of the composition variation.



Appendix 4.6. Tree species relative abundances shifting along the chronosequence that represents time after the first fire. The most abundant tree species in the forest gradually disappear as savanna species arrive and dominate.



Appendix 4.7. Relations between the 'tree community ordination axis 2' and each soil variable. Vertical distances between letters represent their similarity in tree composition. Letters indicate: F – forests; B1 – burnt once; B2 – burnt twice; B2* – old burnt twice; and S – savannas (Appendix 4.3).

Chapter 5

Dispersal limitation as a bottleneck for tree recruitment in burnt Amazonian floodplain forests

Bernardo M. Flores and Milena Holmgren

Abstract

One-seventh of the Amazon basin is covered by floodable ecosystems. These areas host proportionally more savannas than the non-floodable uplands. It has been shown that after a fire on blackwater floodplain forests, soils degrade and tree composition shifts towards dominance of savanna species. This rapid savannization implies that mechanisms such as dispersal limitation, and environmental filtering may favor the recruitment of savanna trees over forest trees.

Here we test the hypothesis that floodplain savannization after fire occurs due to multiple recruitment limitations for forest trees, such as seed availability, degraded soils and competition with herbaceous plants.

First, we sampled seed availability in sites burnt-once, burnt-twice, forests and savannas in an extensive floodplain landscape. Then we experimentally assessed seedling germination, growth and survival of six floodplain pioneer tree species in burnt sites. Species were selected to cover different ecological traits, such as seed mass and root-shoot ratio, and habitat preference: forest, savanna or generalist. With experiments, we analyzed the species performance in contrasting conditions of (1) canopy cover and the root-mat, and (2) number of burns and herbaceous cover. We also compared species performance between forest, edge, and once-burnt sites, and related to their traits.

Although twice burnt sites remained for at least 10 years without tree seeds, we found that experimental forest trees are able to germinate, grow and survive on all conditions. Sapling growth rates increased from the forest to the open once-burnt sites, with a positive effect of seed mass, suggesting that light and nutrients may be important limiting factors. All species grew less on twice-burnt sites, compared to once-burnt sites, possibly limited by poor nutrient conditions. The exception was the savanna tree *H. serratifolium*, which grew and survived well in twice burnt sites, revealing the habitat where it performs better.

Our results show that if seeds of forest trees arrive in burnt floodplain forests, they may thrive despite poor soil conditions, and high herbaceous cover. This finding suggests that dispersal limitation may delay forest recovery after large-scale fires in Amazonian floodplains.

Introduction

The persistence of tropical forests depends on their ability to recover from disturbances (Holling 1996). When disturbances happen, recruitment of new individuals is necessary for the recovery of ecological communities (Connel and Slatyer 1977). Yet recruitment limitation at different stages can delay recovery or even arrest the system in an alternative state (Acacio et al. 2007; Barlow and Peres 2008; Veldman and Putz 2011; Chapter 3). Recruitment limitations can be even stronger if disturbances happen frequently, with severe impacts, and at a large-scale (Turner et al. 1998). For instance, when seed banks are severely damaged, succession depends on the arrival of propagules from undisturbed forests or remnant trees.

When large-scale disturbances cause high tree mortality, a long distance from the source may lower the arrival of propagules to colonize (Turner et al. 1998). In this case, long distance dispersal by other means such as wind or frugivore animals may contribute with new recruits (Clark et al. 2005; Nathan et al. 2008). It has been shown that animal dispersal is more likely to reach suitable habitats at long distances, allowing faster colonization (Howe and Smallwood 1982; Hovestadt et al. 1999; Fragoso and Huffman 2000; Jordano et al. 2007). However, animal dispersal into open disturbed sites is more likely to bring seeds from similar environments than from the closed forest understory (Howe and Smallwood 1982; Ritter et al. 2012). This is because frugivore animals adapted to the forest can be sensitive to open areas with contrasting microclimate, and lack of resources (Pearman 2002; Barlow and Peres 2004; Barlow et al. 2006). Another alternative for pioneer tree species is wind dispersal, yet these are a small proportion of the trees found in wet tropical forests (~6%) (Howe and Smallwood 1982). Dry tropical forests host more wind dispersed trees (~23%) (Howe and Smallwood 1982), and tropical savannas even more (29%) (Hovestadt et al. 1999). Hence, if seed dispersal to severely burnt forests happens mainly by wind, savanna tree seeds may arrive in larger quantities if there are savannas in the surroundings.

During strong drought events, fires can penetrate deep into the wet Amazon forest (Aragão et al. 2007; Flores et al. 2014; Resende et al. 2014; Alencar et al. 2015). The impact of fire is more severe on forests located on floodable terrains (Chapter 2). Post-fire nutrient loss in floodplain forests is also higher, compared to uplands, which may cause environmental filtering, slowing-down forest recovery (Chapter 2). Field assessments in these burnt floodplains revealed that fires can destroy almost the entire forest structure, and facilitate the invasion of herbaceous plants (Chapter 3). In the Negro river region, nearly half of these sites were shown to re-burn within the following decades, trapping floodplains in an open vegetation state (Chapter 3). During this transient phase in which floodplain vegetation persists open, soils degrade and savanna tree species become dominant (Chapter 4).

In savannas, recurrent fire conditions may result in constant nutrient losses (Kauffman et al. 1994; Silva et al. 2013; Pellegrini 2016; Pellegrini et al. 2015). Wildfires are also known to facilitate soil erosion and nutrient leaching by water (Shakesby and Doerr 2006). Not surprisingly, tree species from this biome are known for having lower nutrient demands, compared to forest trees (Bond 2010; Silva et al. 2013; Pellegrini et al. 2015). Savanna trees are more adapted to poor soils for having well developed roots (Canadell et al. 1996; Jackson et al. 1996; Hoffmann and Franco 2003). These roots allow savanna tree seedlings to reach deeper water in desiccating conditions during the dry season. Most forest seedlings die in open dry burnt sites (Nepstad et al. 1996; Hoffmann et al. 2004). Savanna trees are also adapted to co-exist with high cover of herbaceous plants (Bond and Midgley 1995; Sankaran et al. 2004), guaranteeing fuel connectivity to spread fires (Archibald et al. 2009). Hence, deep roots allow savanna trees to survive frequent fires and persist, which for forest trees is unlikely (Hoffmann et al. 2004).

Because forest and savanna trees have such contrasting adaptations, the fast savannization of floodplain forests after fire (Chapter 4) suggests that recruitment limitations may be different for both tree types. We hypothesized three mechanisms; (1) savanna trees are more capable or dispersing seeds into burnt sites with open vegetation, (2) savanna trees outcompete forest trees when the environment becomes harsh with desiccating and low nutrient conditions after fires, or (3) savanna trees outcompete forest trees under high herbaceous cover. It is possible that all three mechanisms happen simultaneously, especially on early life states. If there is dispersal limitation to burnt sites (hypothesis 1), the establishment of seeds that arrive may still be limited by environmental filtering (hypothesis 2) and competition (hypothesis 3). We tested these hypotheses in Amazonian floodplains at the middle Negro river region, representing the most extensive area of tropical blackwater forests in the world. We first quantified the abundance and species richness of tree seeds in the soil seed bank of forests, burnt forests and savannas. We then assessed whether planted seeds and seedlings are capable of germinating, growing and surviving in burnt sites, compared to the forest interior and edge. We also experimentally tested the effects of canopy cover, soil root-mat, herbaceous cover, and number of fires on seedling performance. For the experiments we used six floodplain pioneer tree species, covering a gradient of ecological traits, and habitat preferences (see Appendices 5.1 and 5.2 for species habitats and traits).

Methods

Study area

Floodable ecosystems cover about one-seventh of the Amazon (Hess et al. 2015), and roughly half of them are inundated by black water rivers (Melack and Hess 2010). We studied floodplains at the middle Negro river region, within 50 km of the town of Barcelos in Central Amazon (0^o58S, 62^o55W). Despite low nutrient availability, forests can achieve high biomass (Saatchi et al. 2007; Schöngart and Wittmann 2010), and support the aquatic food chain (Henderson 1990). These ecosystems also host extensive peatlands that if burnt would release carbon to the atmosphere (Lähteenoja et al. 2013).

A root-mat typically protects the soil organic layer in blackwater forests effectively recycling nutrients and preventing nutrient leaching by annual floods (Stark & Jordan 1978, Singer & Araujo-Aguiar 1986). Root-mats occur in 63% of floodplain forests, yet in only 11% of upland forests (dos Santos & Nelson 2013). In dry years, root-mats can easily spread fires that percolate through blackwater forests ignited by camp-fires or upland agricultural sites (Flores et al. 2014; Resende et al. 2014). We used Landsat images for the period 1973-2012 to reconstruct fire history of the middle Negro river floodplain landscape (details of the method on Chapter 3). Using fire history, we studied sites burnt once and twice, as well as unburnt forests and savannas.

Soil seed bank data

We studied the soil seed bank in different habitats across the floodplain landscape, including three unburnt forests, three savannas, and 12 burnt forests. Among the 12 burnt sites, we sampled three transects for each treatment: burnt once three years before, burnt once 15 years before, burnt twice 3 years before, and burnt twice nine years before. Each transect was an independent replicate in a different burnt site (see Chapter 3 for details). Transects were 150 m long, in which we collected three sub-samples of the seed bank at 50 m intervals. For each sub-sample, we collected a soil core of 10 x 15 x 5 cm (length x width x depth) including the surface litter and root-mat. From each sub-sample, we counted the number of seeds and distinguished the morphospecies for all seeds that were intact (not destroyed by fire or predators). The abundance and richness of species per plot was represented by the seeds in all three sub-samples.

Field experiments

We conducted two field experiments to assess the effect of (1) 'tree cover' by comparing forest edge with understory, (2) 'root-mat' above the forest soil, (3) 'herbaceous cover' in burnt sites, and (4) 'number of burns' as indication of soil conditions (see Appendix 5.3). We selected sites burnt once and twice for our experiments (Appendices 5.4 and 5.5).

Study species

We selected six pioneer tree species that are common in the floodplain, yet with distinct habitat preference. Two are common in forests: (1) *Macrolobium acaciifolium* and (2) *Hevea brasiliensis*, three are generalists and are common in burnt sites: (3) *Buchenavia oxycarpa*, (4) *Eschweilera tenuifolia*, and (5) *Duroia gransabanensis*, and one is common in savannas: (6) *Handroanthus serratifolium*. The species we selected based on previous inventories that identified where they naturally occur (Appendix 5.1). They also cover a wide range of ecological adaptations (Appendix 5.2). Their natural occurrences were derived from the same sites where we assessed the tree seed banks. We inventoried all trees above 1 cm in DBH in field plots of 0.6 ha (see Chapter 3 for details). Because recently burnt plots had almost no trees, the six tree species were selected based on data from eight field plots (Appendix 5.6). Species 1 and 4 are known long living pioneers that can live up to 500 years of more (Schongart et al. 2005). All six can grow to large sizes and represent important proportions of the community basal area (Appendix 5.6), which implies that they contribute to important ecosystem functions within their respective habitats (Fauset et al. 2015).

Species ecological traits

Before setting the experiments in January 2014, we randomly selected 10 seeds and 10 seedlings of each species to measure morphological traits that strongly correlate with resource acquisition and survival (Osunkoya et al. 1994; Leishman et al. 2000; Dalling and Hubbell 2002; Lahoreau et al. 2006; Moles and Westoby 2006). We measured seed mass, seedling initial growth investments above and below ground (mass and length), and leaf mass (Appendix 5.2). We dried seeds and seedlings to measure their traits. All seedlings had the exact same age of 3.5 months.

Seed collection and seedling preparation

We collected seeds during the high water season between May and July 2013, respecting the timing of the species' reproductive phenology. Seeds were collected from at least 5 different individuals from the same population. For species 3 to 6, seeds were removed directly from the canopy. For species 1 and 2, seeds were collected floating in the water below the forest canopy where several reproductive individuals occurred. For each species around 1000 seeds were collected. All seeds were kept 2-3 months under the forest shade and below the Negro river water, inside litter-bags. This method protects seeds from predators, and preserves them until water levels drop, breaking their dormancy (Kubitzki and Ziburski 1994).

In late September 2013, we planted 500 seeds of each species in individual bags. These bags were kept in a shade-house (30% light) and were taken care by the local government Agricultural Secretary workers, for seedlings to grow until the start of dry season in January 2014. The remaining seeds from each species (> 500) were maintained below water, to be planted a few months later in January 2014, together with the seedlings produced.

Experiment 1

We assessed the roles of forest 'tree cover' and 'root-mat' on seedling germination, growth and survival in contrasting conditions. For 'tree cover', we compared forest understory vs. forest edge (shade vs. light conditions). The edge was the border between forest and once-burnt area. To test the effect of the forest 'root-mat', we removed this soil layer. Because we could not randomize the light vs. shade conditions, we made a split-plot factorial design, randomizing only where the root-mat was removed.

We spread 10 blocks placed at least 200 m from each other along the forest border with once-burnt area (three years before) (see Appendix 5.5). Each block consisted of 2 pairs of plots, one in the forest interior, and the other on the forest edge less than 100 m apart. For each pair, we randomized which plot would have the root-mat removed. This organic layer was present in the whole area, and we removed it with a hoe.

Each plot (4 x 4 m) was divided in nine equal squares. In six squares we planted the six species. One third of each plot was reserved for planting the seeds in the same order in which we planted the seedlings. For each species we planted four seedlings and five seeds. The order of the species in each plot was randomized for each pair of plots. After planting the seedlings, we measured the height of each individual plant. One year later, after the annual flood pulse, we monitored all plots to assess the proportion of seeds that had germinated, and of seedlings that survived per species. We also measured a second time the height to estimate the mean growth of seedlings planted and germinated per species. We used these response variables to indicate species performance in each condition. We used a two-way ANOVA with the factors 'species' and 'root-mat' nested within the 'habitats' (forest vs. edge), to analyze the data.

Experiment 2

We used a split-plot factorial design to assess the roles of 'number of fires' and 'herbaceous cover' on seedling germination, growth and survival in contrasting conditions. For 'number of fires', we compared sites burnt once with sites burnt twice (see Appendix 5.4 for information). The number of fires reflects nutrient availability, with the twice burnt sites being more nutrient limited (Appendix 5.3). Within the center of each burn scar, we placed 10 pairs of plots spaced by at least 100 m (Appendix 5.5). With each pair, we randomized which plot would have the herbaceous cover removed with a hoe. We planted and monitored the seeds and seedlings in the exact same way we did for Experiment 1. We used a two-way ANOVA with the factors 'species' and 'herbaceous cover' nested within the 'habitats' (once burnt vs. twice burnt), to analyze the data.

Comparison of habitats

We used data from the same plots to compare the species performance between habitats: 'forest interior', 'edge', and 'once burnt site'. We considered habitats as they are, hence forests with root-mat and burnt areas with herbaceous cover. We assumed a gradient of light and nutrient conditions increasing from the forest to the burnt area (Appendix 5.3).

Results

Tree seed bank

Our results show that compared to unburnt forests, a first fire reduces the abundance and species richness of tree seeds in the seed bank to 6 and 23% respectively, and a second fire to 1% and 3% respectively (Fig. 5.1). During almost 10 years after second fire, seed abundance remains close to zero. Forests had on average 38 tree seeds of 19 species. Savannas had on average 5 tree seeds of 5 species.

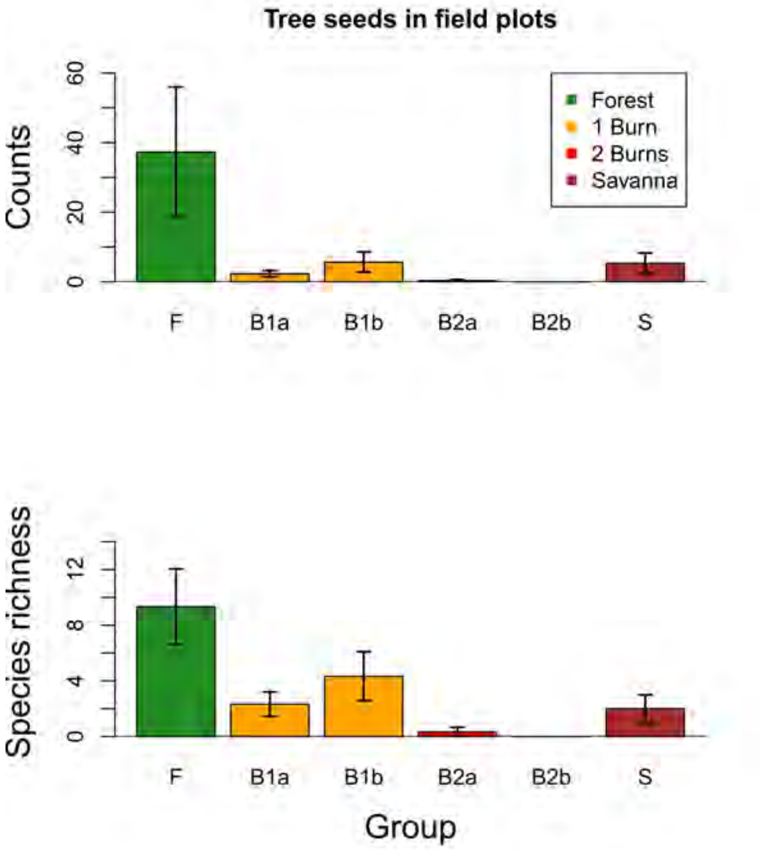


Figure 5.1. Seed availability across habitats (N = 3); forests (F), forests burnt once three years before (B1a), forests burnt once 15 years before (B1b), forests burnt twice three years before (B2a), forests burnt twice nine years before (B2b), and savannas (S).

Experiments

Our Experiment 1 assessed the roles of forest 'tree cover' and 'root-mat' on seed germination and seedling performance. As a general pattern, all six tree species grew more at the forest edge, compared to the forest interior (Fig. 5.2). Root mat removal had no significant effect on seedling germination, survival or growth (Table 5.1). The two long-living pioneers *M. acaciifolium* and *E. tenuifolia* had the highest germination rates, and their survival was higher at the edge compared to the forest interior. For the other forest species, survival was similar inside the forest and at the edge. The typical savanna tree *H. serratifolium* survived less at the edge than below the forest canopy.

Table 5.1. Results from the experiments. Numbers are F-values from the ANOVA. Significance codes (p values): 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

	Sapling survival	Sapling growth	Seed germination	Seedling growth
<u>Experiment 1</u>				
Forest / Edge	10.0 *	31.8 *	0.2	1.8
Rootmat / removed	0.08	0.2	0.3	0.3
Species	13.8 ***	15.0 ***	43.0 ***	30.2 ***
Habitat : species	17.4 ***	9.2 ***	0.9	2.7 *
<u>Experiment 2</u>				
Herb. veg./ removed	0.01	2.7	0.01	0.04
Species	29.2 ***	71.5 ***	37.4 ***	52.8 ***
Habitat : treatment	0.01	4.3 *	0.3	0.4
Habitat : species	12.2 ***	2.6 *	0.4	1.2
<u>Habitat comparison</u>				
Forest / Edge / Burnt	5.1 *	62.8 ***	0.4	11.0 **
Species	9.9 ***	28.9***	30.4 ***	42.1 ***
Habitat : species	8.2 ***	2.9 **	1.3	2.5 **

Our Experiment 2 assessed the roles of 'herbaceous cover' and 'number of fires' (one or two) on seed germination and seedling performance. We found no significant effects of herbaceous cover on seedling germination, survival or growth (Table 5.1). As a general pattern, five of six species grew less on twice-burnt sites compared to once-burnt sites (Table 5.1). The exception was the savanna tree *H. serratifolium* that grew equally well in both habitats (Fig. 5.2). We found different survival patterns among species. The two typical forest species survived more in twice burnt sites and the more generalist species survived less in twice burnt sites. However, these differences were smaller, compared to *H. serratifolium*. This species had a much higher survival in twice burnt sites, compared to once burnt sites.

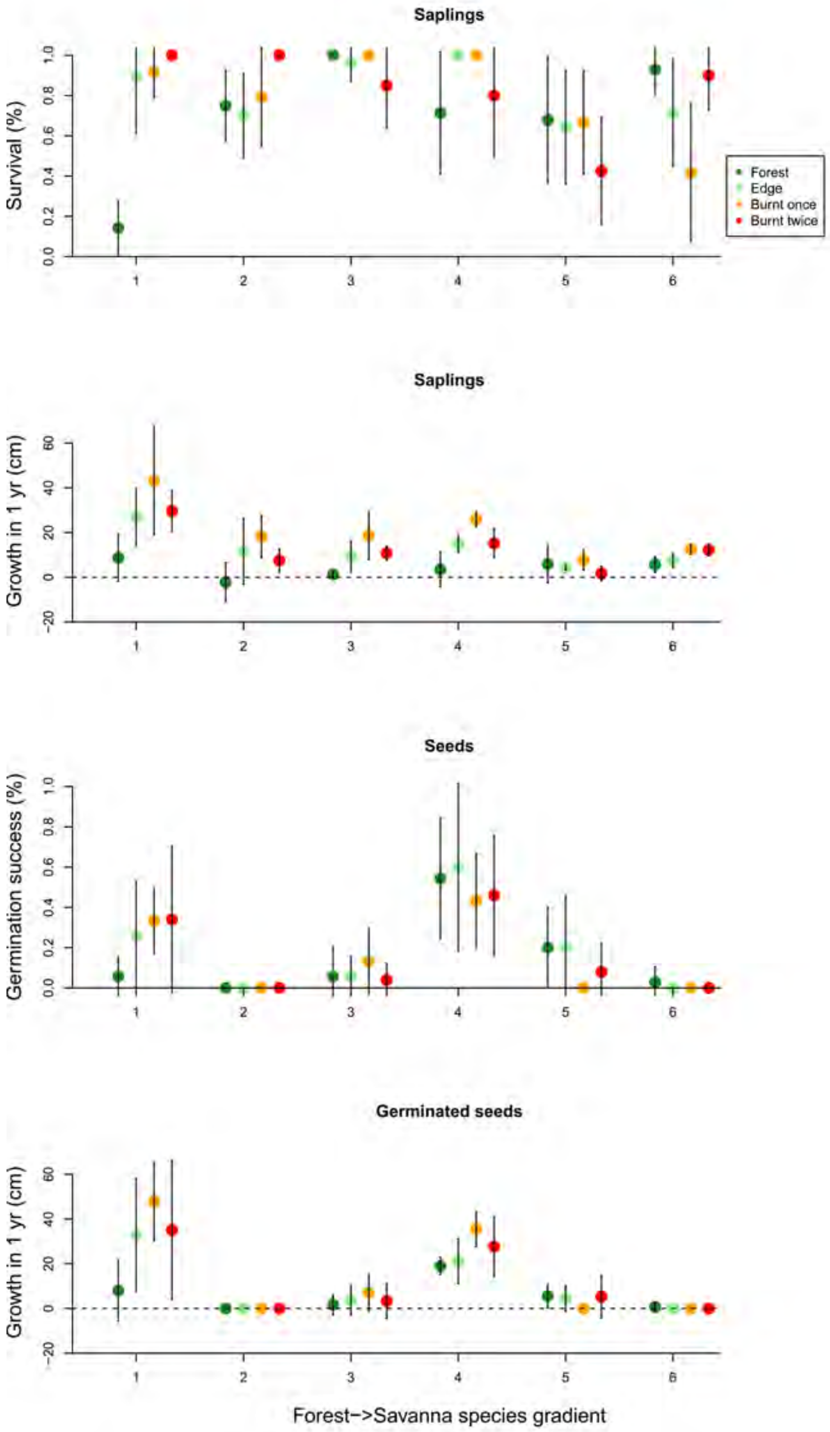


Figure 5.2. Mean (± se) values of our response variables for six tree species ordered by the forest-savanna species rank (see Appendix 5.1). For forest and edge: N = 8; for burnt once: N = 6; burnt twice: N = 10.

We also compared the performance of all six species on three distinct habitats: forest interior, edge, and once-burnt. Survival, and growth of seedlings and saplings were significantly different between habitats, but not seed germination (Table 5.1). Saplings from all species grew faster from the forest, through the edge, towards the open burnt site, with the generalist tree *Duroia gransabanensis* as a single exception (Fig. 5.2).

The comparison of the species performance in relation to their traits revealed that sapling growth rates increased from the forest interior to the open burnt areas, with a positive effect of seed mass (Fig. 5.3). Sapling growth was also marginally predicted by 'forest-savanna species rank' (Appendix 5.1), but not by the 'biomass ratio' (Table 5.2). Seed mass also significantly predicted the species' early life investments on above, below ground, and leaf biomass, yet especially the first (Appendix 5.7).

Table 5.2. Results (*P* values) from statistical analyses between tree species traits and their performance.

	Sapling survival			Sapling growth			Seed germination			Seedling growth		
	Forest	Edge	Burnt	Forest	Edge	Burnt	Forest	Edge	Burnt	Forest	Edge	Burnt
Forest-savanna s	0.20	0.48	0.14	0.77	**0.08**	**0.08**	0.64	0.94	0.28	0.97	0.28	0.28
Biomass ratio	0.28	0.90	0.52	0.50	0.26	0.32	0.59	0.87	0.87	0.85	0.62	0.63
Seed mass	0.12	0.53	0.30	0.90	**0.04**	**0.05**	0.86	0.49	0.24	0.49	0.15	0.13

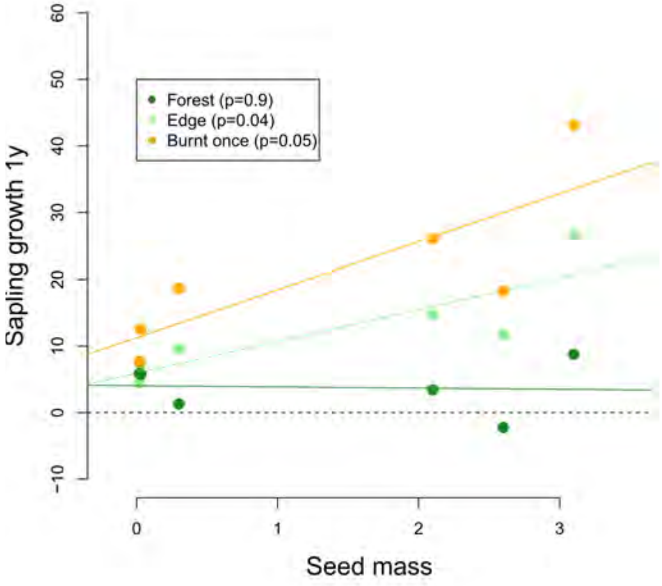


Figure 5.3. Relationship between species average seed mass and one-year sapling growth. Distinct habitats are associated to increasing conditions of light and available phosphorous (Appendix 5.3).

Discussion

Our inventories of tree seed availability show that each fire event depletes even more seed banks of floodplain forests (Fig. 5.1). After the second fire, the lack of seeds persists for at least 10 years, suggesting strong dispersal limitation. Perhaps, seeds brought by water currents (Kubitzki and Ziburski 1994; Parolin et al. 2013) are retained in barriers such as the forest edge, leaving most of the burnt area seedless. It has been shown that two fires in these blackwater forests can undermine their capacity to recover tree structure and diversity (Chapter 3). Perhaps, the persistence of burnt floodplains in an open vegetation state is caused by a positive feedback between seed dispersal and tree recruitment. If burnt areas are unattractive to important tree seed dispersers, forest recovery can be delayed, which maintains dispersal limitation. For instance, forest fires in Amazonian floodplains can trigger a shift in bird communities towards a species composition typical of open areas that lasts for more than 25 years (Ritter et al. 2012). It is possible that comparable shifts occur among other groups of seed dispersers, such as fish and mammal frugivores (Kubitzki and Ziburski 1994; Parolin et al. 2013). This may also apply to water dispersal if seeds floating on the water surface require trees to be retained. Also, because forest destruction is so severe (Flores et al. 2014; Resende et al. 2014; Chapter 3), few trees are left in burnt sites that could provide new seeds, or attract dispersers (Guevara et al. 1986). Nonetheless, if seeds do arrive they will need to overcome environmental filters to germinate and establish.

Our experiments revealed that pioneer trees can germinate, grow well, and survive in burnt sites during their first year of life (Fig. 5.2), which is the most critical phase for tree establishment in Amazonian floodplains (Parolin et al. 2004). This finding is consistent with our hypothesis of dispersal limitation. We found that 20-40% of seeds of the forest tree *Macrolobium acaciifolium*, and 40-60% of seeds of the pioneer tree *Eschweilera tenuifolia* germinated in open burnt areas. Despite these two species being common in forest habitats (Appendix 5.1), they also survived and grew well in burnt areas (Fig. 5.2). Saplings of *M. acaciifolium* grew on average more than 40 cm in one year (Fig. 5.2). This suggests that seeds of this tree are not reaching burnt sites, otherwise they would grow large crowns that facilitate the establishment of other forest species (Hoffmann 1996). This tree produces seeds with high mass (Appendix 5.2), typically in forested areas (Appendix 5.1). Hence, direct dispersal of *M. acaciifolium* by animals is unlikely to reach open burnt areas (Howe and Smallwood 1982; Ritter et al. 2012), and it may require water dispersal (Parolin et al. 2013). If seeds of this tree arrive in burnt sites, our experiments show that they can grow fast, which is likely related to the high availability of resources stored in the seed (Fig. 5.3). The strikingly low survival (< 20 %) of *M. acaciifolium* beneath the forest canopy, compared to open sites (> 80%), coupled with the fact the this pioneer can live for more than 500 years (Schongart et al. 2005), may even suggest that forests with high abundance of this tree may indicate past fire disturbance.

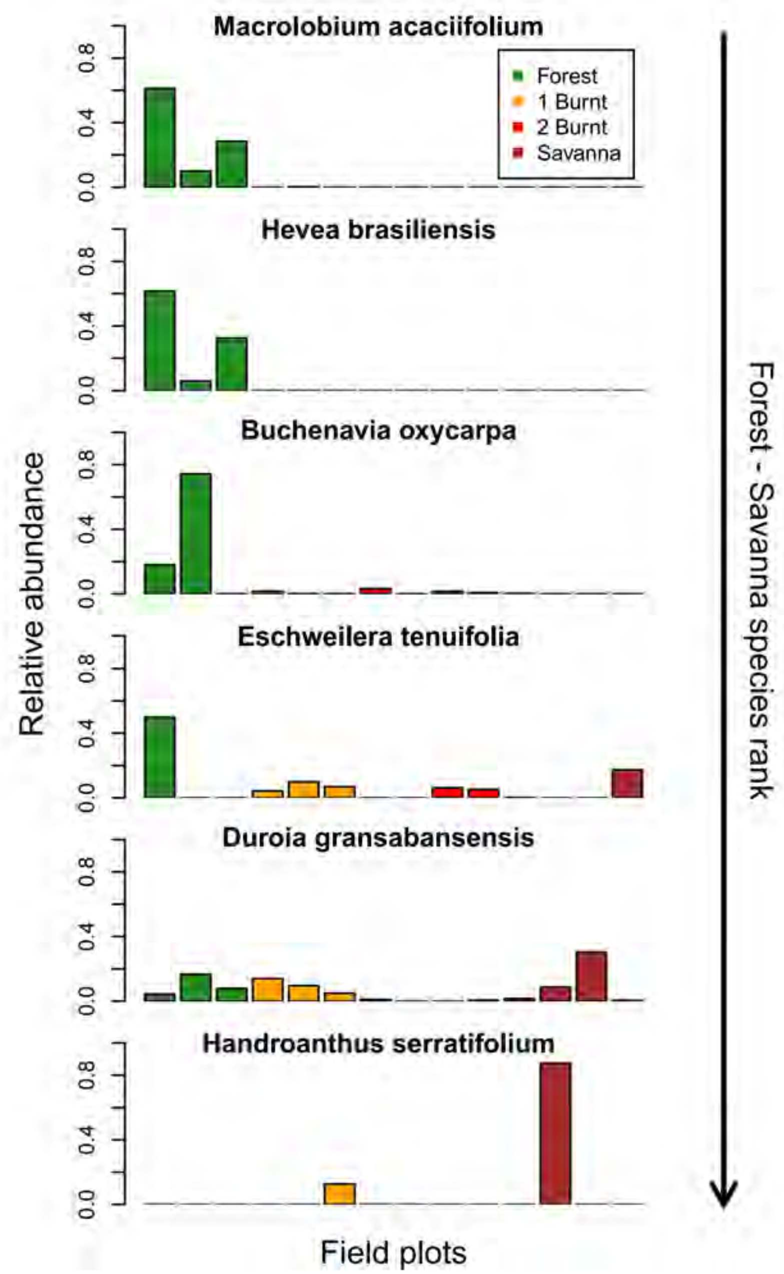
We found that saplings from the six tree species grew better when light conditions increased from the forest interior, through the edge, to the middle of once burnt sites (Fig. 5.2). This contrasts with another study that also found increasing growth rates with light, yet for tree species with lower seed mass (Osunkoya et al. 1994). The reason is that in most cases large seed mass enhances survival and competition under stressing conditions such as shaded habitats (Leishman et al. 2000; Moles and Westoby 2006), or in the low nutrient blackwater floodplains (Parolin et al. 2000). This may help explain why the two typical forest species, *M. acaciifolium* and *H. brasiliensis* had 100% survival in twice burnt sites with poor soil conditions. However, high seed mass may also be beneficial when resources are abundant. In fact, once burnt sites may have ideal conditions for floodplain tree recruitment, with abundant light, and high concentration of available phosphorous and magnesium (Appendix 5.3) probably released by fire (Appendix 5.4).

In sites burnt twice, however, sapling growth of all species was slightly slower than in sites burnt once. An exception was the typical savanna tree *H. serratifolius* that grew equaly fast in once and twice burnt sites (Fig. 5.2). The lower availability of nutrients such as phosphorous and nitrogen in twice burnt sites (Appendix 5.3) may limit the growth of most tree species. It has been shown that after a first fire in these forests, soil nutrients and even clay are gradually washed away during decades (Chapter 4). This is a common process after forest fires across the world (Shakesby and Doerr 2006), yet it seems to last longer in Amazonian floodplains (Chapter 4). Our twice burnt sites had only 10 years since the first fire, when soil conditions are only starting to degrade (Chapter 4). Nonetheless, we found evidence that savanna trees may be more adapted to the soil conditions of twice burnt sites. Probably, the more developed roots of savanna trees, compared to forest trees (Fig. S2) (Canadell et al. 1996; Jackson et al. 1996; Hoffmann and Franco 2003), may allow saplings to nourish from poor soils (Appendix 5.7).

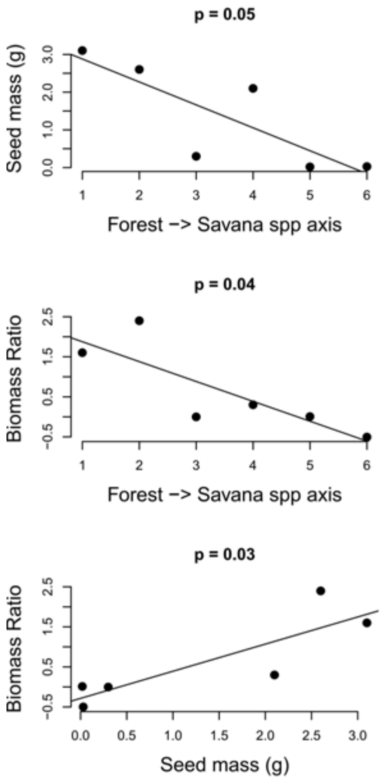
In summary, forest tree recruitment after a second fire may be initially limited by seed dispersal, and if seeds arrive they may be limited by low nutrient availability (hypotheses 1 and 2). Moreover, our results suggest that competition with herbaceous plants is not a limiting factor (hypothesis 3), yet these plants are the main fuel for fires to percolate (van Nes et al. submited). Repeated fires can kill young recruiting forest trees (Hoffmann et al. 2009), and trap the ecosystem with open vegetation (Grady and Hoffmann 2012; Chapter 3). Savanna tree saplings, however, have adaptations to tolerate fire, such as thicker barks (Hoffmann et al. 2009; Hoffmann et al. 2012), and more developed roots (Hoffmann and Franco 2003; Hoffman et al. 2004). Deeper roots of savanna trees are not only an advantage under low resource conditions (Canadell et al. 1996; Jackson et al. 1996), but also under recurrent fire (Bond and Midgley 2001). Therefore, the strategy of savanna trees to co-exist with flammable herbaceous plants (Bond and Midgley 1995; Sankaran et al. 2004), and to maintain poor soil conditions (Paiva et al. 2015), may indirectly reduce competition with forest species. Based on this reasoning, perhaps the high recruitment of savanna trees in burnt sites (Chapter 4) may contribute to accelerate forest savannization in a positive feedback mechanism, yet this hypothesis needs to be addressed in a future study.

Our results indicate that floodplain forest trees seem to have a limited dispersal capacity to open burnt sites. However, it has been shown that within a few decades after fire savanna tree species become dominant (Chapter 4). We may hypothesize that savanna trees with lower seed mass, compared to forest trees, are more capable of dispersing in large quantities into these far open areas (Moles and Westoby 2006; Muller-Landau et al. 2008). For instance, the low seed mass of *H. serratifolius* may facilitate its dispersal by animals such as birds or fish. The open vegetation structure of burnt sites may also attract more animal seed dispersers from the savanna than from the forest (e.g. Ritter et al. 2012). Also, the lower seed mass of savanna trees makes them more likely to be dispersed by wind (Westoby et al. 1996; Hovestadt et al. 1999; Leishman et al. 2000). As a trade-off, smaller seeds are more likely to be predated if they arrive in open areas (Nepstad et al. 1996), and less likely to establish (Moles and Westoby 2006). Therefore, savanna seeds would have to arrive massively in order to promote savannization (Chapter 4).

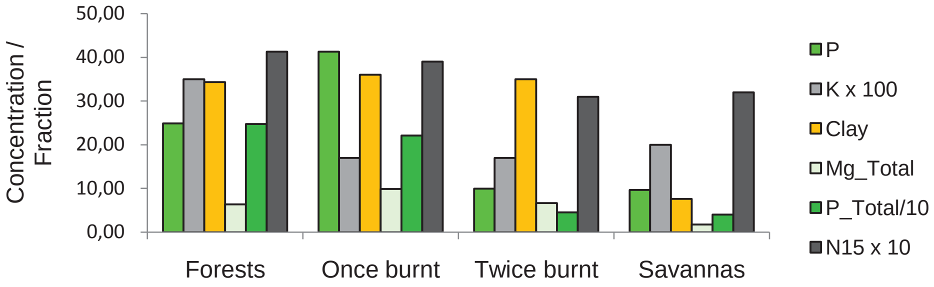
Our combined analyses revealed that dispersal limitation is the first mechanism by which burnt floodplain forests remain trapped in an open vegetation state (Chapter 3). This is surprisining because floodplain trees are known for having many dispersal strategies, including by water and fish (Kubitzki and Ziburski 1994; Parolin et al. 2013). Moreover, tree seeds that are able to arrive in these sites may be limited by poor soil conditions and repeated fires. An implication is that in addition to fire and resources, seed dispersal limitation may be an important mechanism driving forest-savanna transition. This idea also implies that the expantion of savannas may lower forest resilience, if savanna tree species arrive in higher quantities to disturbed sites. Future studies should assess whether selective mechanisms acting on trees with contrasting adaptations can drive forest-savanna transitions in other ecosystems as well.



Appendix 5.1. Proportion of the natural occurrence of tree species used in the experiments across habitats based on field tree inventories.



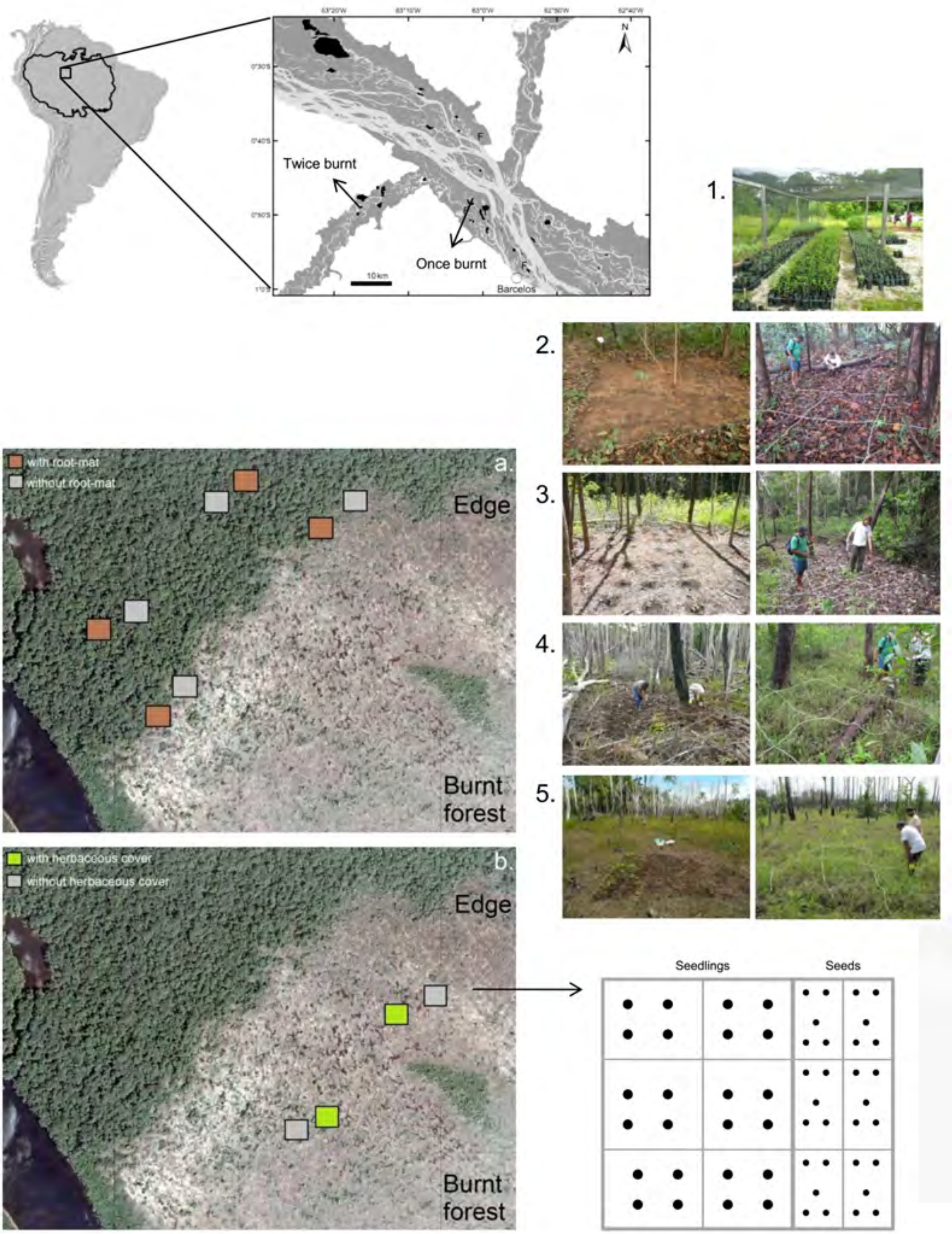
Appendix 5.2. Relationships between species traits. Each circle represents one of the six tree species used in the experiments.



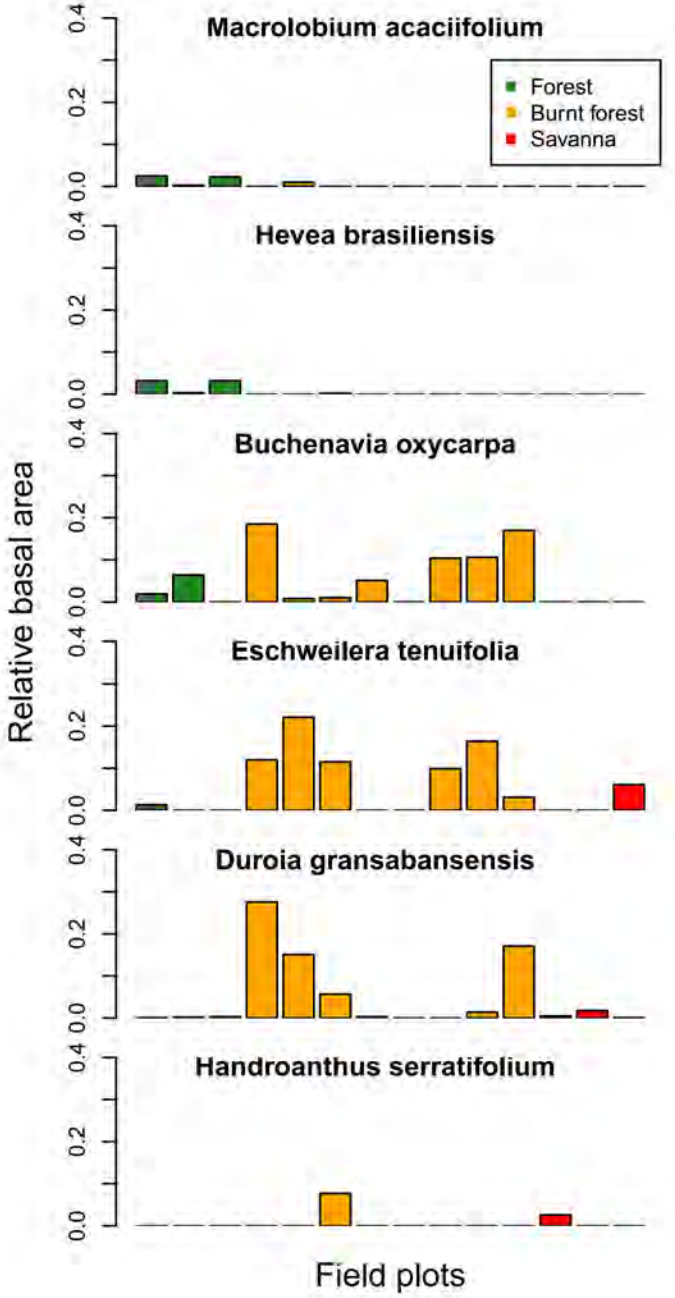
Appendix 5.3. Average nutrient concentrations and clay fraction for the different floodplain habitats used in our experiments.

Appendix 5.4. Information on burnt areas used in the experiments.

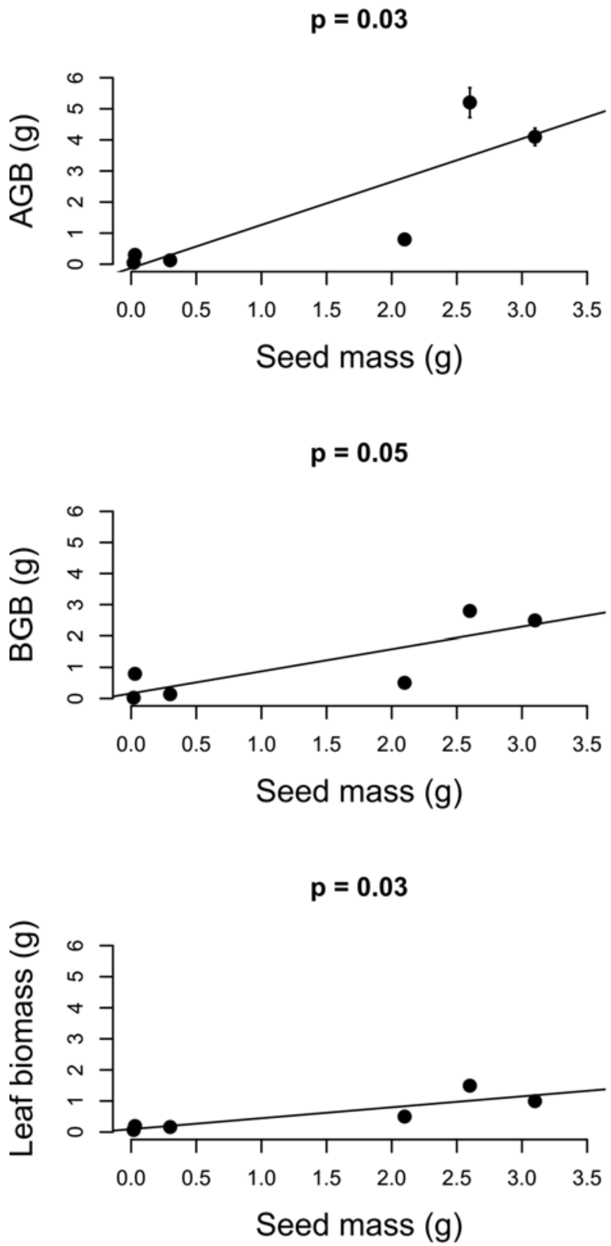
Site	Number of fires	Time since 1st fire (yr)	Time since 2nd fire (yr)	Dry phase length (days.year^{-1})
BC	1	3	3	172
BD	2	10	3	165



Appendix 5.5. Sampling design for field experiments; (a) experiment 1, and (b) experiment 2. The location of each species was randomized for each pair of plots, and the order was reproduced for seeds and seedlings. Photos: 1. all seedlings in the shade-house a few days before setting the experiments; 2. Forest, 3. Edge, 4. Once-burnt, 5. Twice-burnt; removal on left and control on right photos.



Appendix 5.6. Basal area of the tree species used in the experiments, relative to the basal area of the whole tree community. Data obtained from field inventories across habitats.



Appendix 5.7. Relationship between seed mass of tree species with their initial investments in biomass.

Chapter 6

Synthesis

Bernardo M. Flores

Natural ecosystems are characterized by a tremendous complexity of habitats, interactions, and processes. A simple walk in nature can inspire a wealth of hypotheses about the forces that could drive ecosystem change. Understanding these forces is especially important when it comes to systems with alternative basins of attraction (Scheffer et al. 2001). With a simplified perspective of reality, mathematical models may show potential implications of nonlinear interactions. Empirical evidence can reveal mechanisms at multiple scales that drive these nonlinearities. Experiments are a powerful way to scrutinize such ideas but unavoidably restricted scale. In my thesis, inspired by the theory of 'ecological resilience' (Holling 1973), I combine field observations, remotely sensed data and field experiments to build a better understanding of the role of floodplain ecosystems in shaping the resilience of the Amazon forest.

The Amazon basin is predominantly covered by forests. Nonetheless, extensive savannas occur along the north and south extremes, and islands of savanna can be found throughout the whole basin (Prance 1996). This massive Amazonian system as we know it today is the result of more than 12 million years of fluvial, sedimentation and vegetation dynamics (Hoorn et al. 2010). Mega wetlands covering most of the western Amazon began to retreat with the formation of the Amazon river 7 million years ago. Currently, the basin has 20% of the world's freshwater flowing continuously through a dense network of rivers. A strong rainfall seasonality produces a flood wave (Richey et al. 1989) that inundates one seventh of the Amazon every year (Hess et al. 2015).

To understand the resilience of this complex ecosystem, I split it into two contrasting forms that dominated its geomorphological history, floodplains and uplands. I tested the hypothesis that Amazonian forests on floodplains are less resilient than forests on uplands, and hence more likely to shift into a savanna state. Although previous studies found some evidence to support this idea, they were restricted to the central Amazon region (Flores et al. 2014; Resende et al. 2014). Also, the mechanisms responsible for forest-savanna transition were unknown. I expanded these previous efforts to the whole Amazon basin. Using resilience indicators (Scheffer et al. 2015b), such as the analysis of tree cover frequency distributions and the measure of recovery rate from perturbations, I assessed how forest resilience changes with drought and fire. In the field I measured changes in the forest soil and tree composition to test the savannization hypothesis, and developed experiments to assess the mechanisms behind such transition.

Evidence from basin-wide tree cover data

As briefly explained in **Chapters 1** and **2**, the frequency distribution of tropical tree cover has revealed alternative attractors that correspond to forest and savanna (Hirota et al. 2011; Staver et al. 2011). Although tree cover is analysed in one moment in time, spatial patterns reflect long-term vegetation dynamics. If forests on floodplains are indeed less resilient than forests on uplands, the analyses of tree cover should reveal a relatively higher proportion of savannas in the floodplains. In **Chapter 2**, I found that tree cover density distribution of floodplains is bimodal, with savannas covering 34% of the seasonally flooded Amazon. In contrast, tree cover density distribution for Amazonian uplands has only one mode corresponding to forest. These patterns do not imply that all Amazonian savannas are located on floodplain ecosystems. In fact, 56% of all Amazonian savannas occur on uplands, yet these savannas cover only 7% of the massive upland ecosystem. What our results suggest is actually a higher probability that floodplains may be trapped in the savanna basin of attraction, compared to uplands.

The relative resilience of forest and savanna also changes as a function of annual rainfall (Hirota et al. 2011). At critical rainfall values, known as tipping points, the entire system may collapse to the alternative state. The tipping point for tropical forests has been estimated at ~ 1000 mm of annual rainfall, which means that below this threshold, forests are expected to be rare (Hirota et al. 2011; Staver et al. 2011). In **Chapter 2**, the broad-scale analyses of tree cover as a function of rainfall support the tipping point for upland forests at 1000 mm, yet revealed a strikingly higher rainfall threshold for floodplains at 1500 mm. This finding has direct implications for floodplain forest resilience in the face of climate change. If the Amazonian climate dries as predicted (Lau and Kim 2015), with ENSO events happening more frequently (Cai et al. 2014), floodplain forests may be the first to collapse, expanding the savanna biome across the basin. Up to now, the expansion of savannas have been assumed to occur from the borders of the Amazon basin into the core region (Malhi et al. 2009). My research suggests that floodplain ecosystems may act as an 'Achilles-heel' of the Amazon forest system, increasing the pervasiveness of the savanna biome.

One may think that floodplains and uplands are so different that the presence of savannas in one ecosystem would not be contagious to the other. Nonetheless, connectivity between floodplains and uplands may allow savannas to spread. For example, it has been shown for Africa and central Amazon that floodplains can spread fires into the uplands (Heinl et al. 2007; Resende et al. 2014). Across the Amazon basin, neighbouring floodplains and uplands also share in average more than 30% of tree species (Terborgh and Andresen 1998; Wittmann et al. 2006), suggesting a history of species exchange. Such connectivity implies that floodplain fires may penetrate upland forests in drier years, and that the dispersal of savanna plant species may potentially assist the transition to savanna. Studies that address such connectivity at the landscape scale can greatly contribute to our understanding of what drives biome expansion.

Evidence from recovery rates after fire

The speed at which a perturbed system recovers back to the original state suggests it's capacity to persist (Holling 1973). A faster recovery implies that the system is less likely to be trapped in the alternative basin of attraction (van Nes and Scheffer 2007). In tropical terrestrial ecosystems, frequent fires may trap the vegetation in an open state by limiting the recruitment of forest trees (Grady and Hoffmann 2012; Murphy and Bowman 2012). In **Chapter 2**, I show at a basin-wide scale that the fast recovery of tree cover in uplands contrasts sharply with the lack of recovery in floodplains after fire, suggesting a pattern of lower floodplain resilience. Field validation with data on tree basal area support the satellite patterns, showing that uplands quickly recover forest structure, whereas floodplains remain open for a long time (see Fig. 6.1). Although these patterns indicate essentially the recovery of forest structure and canopy closure, they have direct implications for flammability and risk of ecological transition.

Field data for Central Amazonian floodplains rendered insights on what limits forest recovery. After a second fire event, recovery of tree basal area and of the forest root mat slows down abruptly, indicating that resilience is being lost (**Chapter 3**). Such loss of forest resilience makes floodplain ecosystems highly susceptible to the fire trap (Grady and Hoffmann 2012). Evidence of slowing down forest recovery has also been shown for Amazonian uplands following repeated land-use (Jakovac et al. 2015), and forest fires (Barlow and Peres 2008). Under recurrent fire, however, upland forests seem to persist with an apparently unlimited capacity to recover canopy closure (**Chapter 2**). This pattern is also reflected in the fast recovery of biomass across the Amazon basin following various forms of land-use (Poorter et al. 2016).

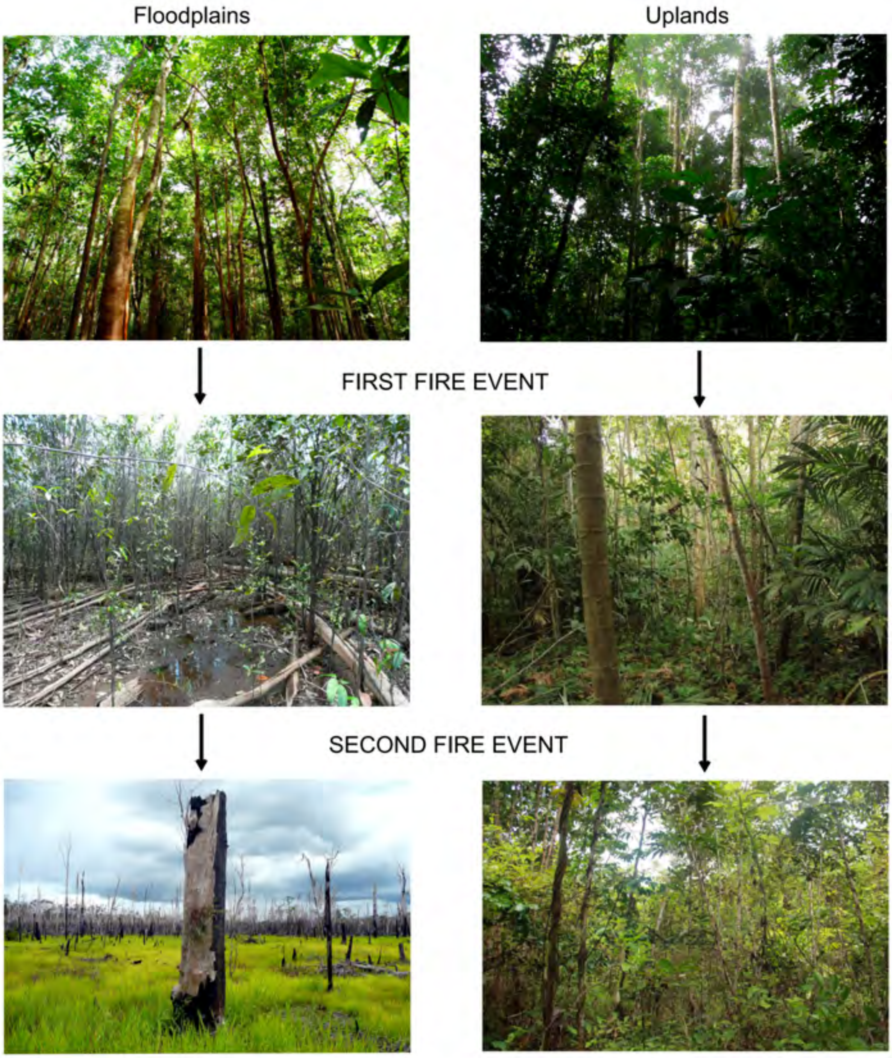


Figure 6.1. Photos contrasting the recovery of floodplain and upland forests under recurrent fire. Top: unburnt forests; middle: forest succession with 15 years in the floodplain, and 8 years in the uplands; lower: forest succession with 9 years in both systems. Photo credits to Catarina Jakovac for upland secondary forests; B. M. Flores for other photos.

Soil degradation after fire

One reason for the contrasting resilience of floodplain and upland forests may be related to their resistance to soil degradation after fire (**Chapter 2**). Floodplain forests quickly lose soil nitrogen, phosphorous and even clay, whereas upland forests preserve most of the original soil fertility. This difference may be caused by a combination of two factors. First, the more destructive impact of fire on floodplain forests, compared to upland forests (Resende et al. 2014; **Chapter 2**), implies that more nutrients and sediment can be washed away. Second, post-fire erosion is more intense in floodplains due to the seasonal inundation, whereas upland soils erode during runoff episodes following heavy rain.

Soil erosion by water runoff is common in burnt forests across all continents (Prosser and Williams 1998; Thomas et al. 1999; Wondzell and King 2003; Shakesby and Doerr 2006). For instance, fire can destroy the litter cover, leading to more intense runoff and sediment transport at local scales (Prosser and Williams 1998). These authors propose a framework, in which a 'window of disturbance' starts with fire and ends when both litter and vegetation recover, and in the meanwhile challenges the ecosystem's resistance to erosion. Perhaps, forest resilience may also depend on the capacity to resist erosion under a wide range of leaching conditions. Forests that lose soil fertility too fast are more likely to fail in recovering forest structure as well. The case of Amazonian floodplains exemplifies how the rates of soil degradation and forest recovery may interact, as soil erosion continues during a long 'window of disturbance'. In uplands, erosion intensity may depend on other factors such as topography, and the 'window of disturbance' is rather ephemeral (**Chapter 2**) (see Fig. 6.2).

Forest recovery rate after fire is thought to be determined by resource availability across landscapes, implying that low resource environments are more likely to be trapped in a savanna state (Kellman 1984; Lehmann et al. 2011; Hoffmann et al. 2012; Murphy and Bowman 2012). Patterns shown in **Chapters 2** and **4**, however, support the idea that soil may change within ecological time-scales, and thus should be treated as a condition that varies in space and time. In this view, the speed at which a soil degrades after fire may be more determinant for forest resilience than its resource availability before fire. To illustrate this hypothesis, the superficial soil of floodplain forests had more nitrogen and the same amount of phosphorous compared to the soil of upland forests before fire. This could lead to the wrong prediction that floodplain forests are more likely to recover from perturbations.

However, after fire the loss of these nutrients was much faster in the floodplains, revealing one potential reason for this ecosystem's fragility (**Chapter 2**). The perception that soils change with the vegetation is evident in most studies of forest encroachment in savanna landscapes (Silva et al. 2008; Coetsee et al. 2010; Silva and Anand 2011; Pellegrini et al 2014; Pellegrini et al. 2015), and should also be taken into account in studies that address forest savannization.

Mechanisms for forest savannization

In **Chapter 4,** I show that floodplain forests can shift into a true savanna state within a few decades from the first fire. Upland forests require centuries of chronic perturbation by recurrent fire to go through the same shift (Cavelier et al. 1998). This is because seasonal flooding seems to reduce forest resilience and accelerate the transition to savanna in at least two ways (Fig. 6.2). First, flooding restricts the time in which trees can grow (Schongart et al. 2002), slowing down forest recovery. Second, flooding intensifies soil degradation, creating an environmental filter that selects for savanna tree species (Bond 2010; Silva et al. 2013; Paiva et al. 2015; Pellegrini 2015). The recruitment of savanna trees adapted to co-exist with fire, may also contribute to accelerate forest savannization, for instance by promoting fires that kill forest trees (Bond and Midgley 1995). Future studies that assess changes in plant functional types after fire in different forest ecosystems can help improve our understanding of other forces that may drive forest-savanna transitions.

Across many parts of the tropics, yet especially in South America, savannas are found to have relatively poorer soils compared to nearby forests (Bond 2010; Veldman and Putz 2011; Wood and Bowman 2012; Dantas et al. 2013;Silva et al., 2013; Lehmann et al. 2014; Paiva et al. 2015; Pellegrini 2015; Veenendaal et al. 2015). It seems logic that the transition from forest to savanna must involve soil degradation. Along this transition, an environmental filter emerges selecting for plant species that are more adapted to the new soil conditions. Savanna tree species are more adapted to lower soil fertility, whereas forest species demand more nutrients to build up forest biomass (Bond 2010; Silva et al. 2013; Paiva et al. 2015; Pellegrini 2015). Savanna trees have more developed roots than forest trees (Canadell et al. 1996; Jackson et al. 1996), which may allow compensating for nutrient and moisture limitations (Bond 2008). Savanna trees also contribute to maintain poor soil fertility for providing litter inputs to the soil with low nutrient content, whereas forest trees fertilize the soil with nutrient rich litter

(Paiva et al. 2015). Therefore, the soil and tree compositional shifts in burnt floodplains characterize a classical forest savannization (**Chapter 4**). The transition from clayey to sandy soils in burnt floodplains may also be a hint to the origin of Amazonian sandy savanna islands, especially those located on palaeo-rivers (Rossetti et al. 2012).

Another important mechanism for savannization is related to the arrival of forest and savanna trees in disturbed sites. Savannas are defined by the co-existence between trees and grasses (Scholes and Archer 1997). Therefore, savannization depends on the recruitment of savanna tree species. In burnt floodplains, savannization can in part be explained by environmental filtering (**Chapter 4**), yet it could also be that savanna trees are more capable of dispersing into open sites than forest trees. For instance, when floodplain forests burn for the first time, bird community composition shifts towards dominance of species typical of open areas (Ritter et al. 2012). If birds are important seed dispersers moving from sites with open vegetation, savanna tree seeds may be more likely to arrive. The same pattern may occur with other animals adapted to habitats with closed understory (Hovestadt et al. 1999). In **Chapter 5**, I show that planted seeds of forest trees germinated and grew well in burnt floodplains, indicating dispersal limitation. Perhaps forest trees with larger seeds are less capable of dispersing far into disturbed sites than savanna trees with smaller seeds (Muller-Landau et al. 2008). While forest trees are mostly animal dispersed, savanna trees are commonly wind dispersed (~ 30%) (Hovestadt et al. 1999). Therefore, if savanna species are part of the regional pool (Ricklefs 1987), the risk of savannization is expected to be higher. For instance, the Negro river floodplain landscape includes several islands of savanna (Prance 1996; Junk et al. 2011) from where seeds can arrive (**Chapter 4**). The same idea applies to the risk of forest encroachment in a savanna landscape, and may help explain why disturbed upland forests in the Central Amazon are so persistent.

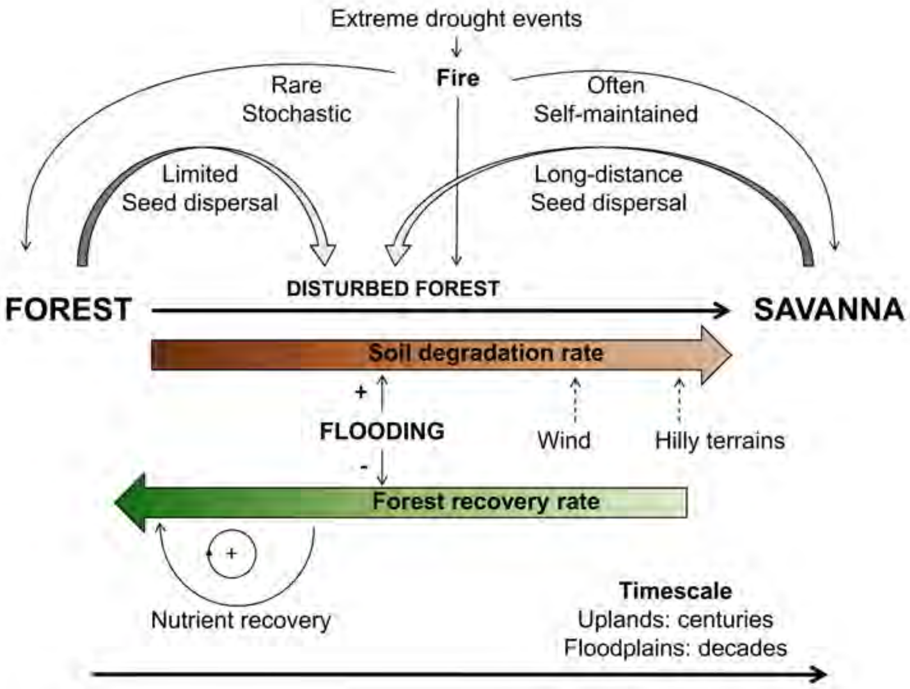


Figure 6.2. Mechanisms driving forest-savanna transition in Amazonian ecosystems. Flooding accelerates the transition by reducing forest recovery rate and enhancing soil degradation rate.

Risks and implications of ecological transitions

While global temperature increases gradually, some ecosystems may respond abruptly, usually with catastrophic consequences for societies (Scheffer et al. 2001). This risk becomes even higher in wet tropical regions where species are less adapted to climatic variation than species from temperate regions, and therefore less likely to tolerate the impact of climate change (Perez et al. 2016). Global warming may have already enhanced the frequency of extreme El Niño events (Cai et al. 2014), leading to more severe forest fires in the Amazon (Brando et al. 2014). Such stochastic perturbations will become a frequent test to the resilience of Amazonian forests.

Drought episodes are associated with massive spread of wildfires in both floodplain and upland tropical forests (**Chapter 2**; Aragão et al. 2007; Flores et al. 2014; Resende et al. 2014; Alencar et al. 2015). Floodplain forests are surprisingly flammable due to the accumulation of fuel in the form of a root-mat (dos Santos and Nelson 2013), and to a relatively more open understory (Resende et al. 2014). Upland forests can percolate fire with less severe impact on tree cover (**Chapter 2**), yet other factors such as deforestation, logging and drought can reduce tree cover and increase upland forest flammability (Nepstad et al 1999; Brando et al. 2014).

The results discussed in this thesis have major implications. As drought and fire episodes become more frequent, floodplain forests may become more vulnerable to shift into a savanna state. Expansion of floodplain savannas might in turn accentuate the risk of upland forest savannization at the heart of the Amazon. This implies that protecting floodplain forests from fire during drought episodes may substantially contribute to protect the entire Amazonian system from savanna expansion. The moment when fire penetrates a tropical forest may be the onset of ecological transition. Such transitions may unfold depending on several conditions, such as fire frequency, fire severity, leaching intensity, and the availability of forest and savanna species in the region. For instance, fire makes a forest more flammable and more likely to burn again (Cochrane et al. 1999). Fire releases nutrients and sediments that can be washed away by hydrological processes (Shakesby and Doerr 2006), challenging the forest's ability to persist in the long-term. When savanna species start to arrive they may constantly supply propagules, increasing savanna pervasiveness, and promoting flammability that excludes forest species (Bond and Midgley 1995).

Societies that wish to conserve tropical forests and savannas must manage fire. Savannas are extremely important for their biodiversity and ecosystem services (Parr et al. 2014; Bond 2016). Their conservation usually requires strategic fire management at the landscape scale (Durigan and Ratter 2016). Forests are important for the same reasons (Putz and Redford 2010), and in addition they contribute to regulate climate regionally and globally. Their conservation requires fire prevention. Scientists can predict fire occurrence (Chen et al. 2011), and its impact on both biomes, whereas practical knowledge of indigenous populations, who shaped nature with fire for thousands of years, is key to develop the correct strategy (Mistry et al. 2016). The development of a fire management policy that combines scientific and ancient knowledge may generate long-term benefits for the society and the environment of tropical regions.

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Summary

The Amazon has recently been portrayed as a resilient forest system based on quick recovery of biomass after human disturbance. Yet with climate change, the frequency of droughts and wildfires may increase, implying that parts of this massive forest may shift into a savanna state. Although the Amazon basin seems quite homogeneous, 14% is seasonally inundated. In my thesis I combine analyses of satellite data with field measurements and experiments to assess the role of floodplain ecosystems in shaping the resilience of Amazonian forests.

First, I analyse tree cover distribution for the whole Amazon to reveal that savannas are relatively more common on floodplains. This suggests that compared to uplands, floodplains spend more time in the savanna state. Also, floodplain forests seem to have a tipping point at 1500 mm of annual rainfall in which forests may shift to savanna, whereas the tipping point for upland forests seems to be at 1000 mm of rainfall. Combining satellite and field measurements, I show that the higher frequency of savannas on floodplain ecosystems may be due to a higher sensitivity to fire. After a forest fire, floodplains lose more tree cover and soil fertility, and recover more slowly than uplands **(chapter 2)**.

In floodplains of the Negro river, I studied the recovery of blackwater forests after repeated fires, using field data on tree basal area, species richness, seed availability, and herbaceous cover. Results indicate that repeated fires may easily trap blackwater floodplains in an open-vegetation state, due the sudden loss of forest resilience after a second fire event **(chapter 3)**.

Analyses of the soil and tree composition of burnt floodplain forests, reveal that a first fire is the onset of the loss of soil fertility that intensifies while savanna trees dominate the tree community. A tree compositional shift happens within four decades, possibly accelerated by fast nutrient leaching. The rapid savannization of floodplain forests after fire implies that certain mechanisms such as environmental filtering may favor the recruitment of savanna trees over forest trees **(chapter 4)**.

In **chapter 5,** I experimentally tested in the field the roles of dispersal limitation, and environmental filtering for tree recruitment in burnt floodplain forests. I combine inventories of seed availability in burnt sites with experiments using planted seeds and seedlings of six floodplain tree species. Repeated fires strongly reduce the availability of tree seeds, yet planted trees thrive despite degraded soils and high herbaceous cover. Moreover, degraded soils on twice burnt sites seem to limit the growth of most pioneer trees, but not of savanna trees with deeper roots. Our results suggest a limitation of forest trees to disperse into open burnt sites.

The combined evidence presented in this thesis support the hypothesis that Amazonian forests on floodplains are less resilient than forests on uplands, and more likely to shift into a savanna state. The lower ability of floodplains to retain soil fertility and recover forest structure after fire, may accelerate the transition to savanna. I also present some evidence of dispersal limitation of floodplain forest trees. Broad-scale analyses of tree cover as a function of rainfall suggest that savannas are likely to expand first in floodplains if Amazonian climate becomes drier. Savanna expansion through floodplain ecosystems to the core of the Amazon may spread fragility from an unsuspected place.

Resumo

A Amazônia foi recentemente mostrada como um sistema florestal resiliente por apresentar uma rápida recuperação da biomassa após a perturbação humana. Entretanto, mudanças climáticas podem aumentar a freqüência de secas e incêndios, o que implica na possibilidade de que uma parte dessa imensa floresta mude para o estado de savana. Apesar da bacia Amazônica parecer razoavelmente homogênea, 14% inunda sazonalmente. Na minha tese, combino análises de dados de satélite com medidas e experimentos em campo para acessar o papel desses ecossistemas inundáveis em moldar a resiliência da floresta Amazônica.

Primeiro, eu analiso a distribuição de cobertura de arvores em toda a Amazônia para revelar que savanas são mais comuns nessas planícies inundáveis. Esse padrão sugere que comparadas à terra-firme, áreas inundáveis passam mais tempo no estado de savana. Ainda, florestas inundáveis parecem ter um limiar em 1500 mm de chuva anual no qual podem virar savanna, enquanto que esse limiar para a terra-firme parece ser em cerca de 1000 mm de chuva. Combinando medidas usando imagens de satélite e em campo, eu mostro que a maior freqüência de savanas em ecossistemas inundáveis pode ser devido à uma maior sensibilidade ao fogo. Após um incêndio florestal, áreas inundáveis perdem mais cobertura de árvores e fertilidade do solo, e recuperam mais lentamente que em terra-firme **(capitulo 2)**.

Em planícies de inundação do Rio Negro, eu estudei a recuperação florestal após fogo repetido usando dados de campo da área basal de árvores, riqueza de espécies, disponibilidade de sementes e cobertura herbácea. Os resultados indicam que o fogo repetido pode facilmente aprisionar florestas inundáveis por água preta em um estado de vegetação

aberta devido a perda repentina da resiliência florestal após o segundo fogo **(capitulo 3)**.

Analises do solo e da composição de árvores em florestas inundáveis revelam que o primeiro fogo inicia um processo de perda da fertilidade do solo que intensifica enquanto árvores de savana passam a dominar a comunidade. Essa mudança na composição de árvores ocorre em menos de quatro décadas, possivelmente acelerada por uma rápida lixiviação dos nutrientes do solo. A rápida savanização de florestas inundáveis após o fogo implica na existência de mecanismos que favoreçam o recrutamento de árvores de savana, como por exemplo filtros ambientais **(capitulo 4).**

No **capitulo 5** eu testo experimentalmente no campo o papel da limitação de dispersão e de filtros ambientais para o recrutamento de árvores em florestas inundáveis após o fogo. Eu combino inventários de sementes de árvores nesses locais queimados, com experimentos usando sementes e mudas plantadas de seis espécies de árvores que ocorrem nesse ecossistema. O fogo repetido reduz fortemente a disponibilidade de sementes de árvores, mas essas tem sucesso quando plantadas apesar da presença de um solo degradado e alta cobertura herbácea. Ainda, solos degradados em locais que queimaram duas vezes parecem limitar o crescimento da maioria das espécies de árvores, mas não de árvores de savana com raízes profundas. Nossos resultados sugerem uma limitação das árvores de floresta em dispersar para locais queimados e abertos.

O conjunto das evidências apresentadas nessa tese sustentam a hipótese de que florestas inundáveis da Amazônia são menos resilientes que florestas de terra-firme, e mais propensas à mudar para o estado de savana. A pouca habilidade que essas florestas têm em reter a fertilidade do solo e recuperar a estrutura florestal após o fogo, pode acelerar a transição para savana. Também apresento evidência de que árvores de florestas inundáveis possuem limitação de dispersão. Análises em larga escala espacial da cobertura de árvores em função da quantidade de chuva anual sugerem que savanas são mais propensas a expandir primeiro nas áreas inundáveis se o clima da Amazônia ficar mais seco. A expansão de savanas por ecossistemas inundáveis para o cerne da Amazônia poderia espalhar fragilidade de um local inesperado.

Samenvatting

De Amazone is recentelijk voorgesteld als een veerkrachtig bossysteem vanwege het snelle herstel van haar biomassa na menselijke verstoring. Echter, door klimaatverandering kan de frequentie van droogtes en branden toenemen, wat betekent dat delen van dit gigantische bos kunnen veranderen in een savannetoestand. Hoewel het Amazonestroomgebied behoorlijk homogeen lijkt, overstroomt 14% ervan jaarlijks. In mijn proefschrift combineer ik analyses van satellietgegevens met veldmetingen en -experimenten om de rol van zulke overstromingsvlakte-ecosystemen in de veerkracht van bossen in de Amazone te bepalen.

Eerst analyseer ik de verdeling van bosbedekking voor de gehele Amazone en onthul dat savannes relatief vaak voorkomen in overstromingsvlaktes. Dit geeft aan dat vergeleken met hooglanden de overstromingsvlaktes veel tijd in de savannetoestand verkeren. Ook lijken bossen in overstromingsvlaktes een kantelpunt te hebben bij 1500 mm jaarlijkse regenval waarbij bossen veranderen in savanne, terwijl het kantelpunt voor bossen in hoogvlaktes lijkt te liggen bij 1000 mm jaarlijkse regenval. Door satelliet- en veldmetingen te combineren laat ik zien dat het vaker vóórkomen van savannes in overstromingsvlaktes mogelijk wordt veroorzaakt door een hogere frequentie van branden. Overstromingsvlaktes verliezen na een bosbrand meer bosbedekking en bodemvruchtbaarheid, en herstellen minder snel, dan hoogvlaktes (**hoofdstuk 2**).

In overstromingsvlaktes van de rivier de Negro heb ik het herstel van bossen na herhaaldelijke branden bestudeerd, gebruikmakend van veldgegevens over het grondvlak van bomen, soortenrijkdom, zadenbeschikbaarheid en de bedekking door kruidachtige planten. De resultaten wijzen erop dat herhaaldelijke branden deze zwartwateroverstromingsvlaktes in een openvegetatietoestand houden door het plotselinge verlies aan veerkracht van het bos na een tweede brand (**hoofdstuk 3**).

Analyses van de bodem- en bomensamenstelling van verbrande bossen in overstromingsvlaktes onthullen dat een eerste brand het begin betekent van een geleidelijk verlies aan bodemvruchtbaarheid dat sterker wordt wanneer savannebomen de bomengemeenschap domineren. Een verandering in de samenstelling van bomen vindt plaats binnen vier decennia, mogelijk versneld door snelle uitspoeling van nutriënten. De snelle savanne-uitbreidingin bossen in overstromingsvlaktes na vuur impliceert dat bepaalde mechanismen zoals filtering door omgevingsvariabelen gunstiger zijn voor de aanwas van savannebomen dan voor bosbomen (**hoofdstuk 4**).

De invloed van dispersielimitatie en filtering door omgevingsvariabelenop de aanwas van bomen in verbrande bossen in overstromingsvlaktes werd experimenteel getest in het veld. Ik combineerde inventarisaties van zadenbeschikbaarheid op verbrande plaatsen met experimenten, gebruikmakend van geplante zaden en zaailingen van zes boomsoorten uit overstromingsvlaktes. Herhaalde branden verminderen de beschikbaarheid van boomzadensterk, maar ondanks verarmde bodems en hoge bedekking van kruidachtigengedijen geplante bomen er toch. Bovendien lijken verarmde bodems op tweemaal verbrande plaatsen de groei van de meeste pionierbomen te beperken, maar niet die van savannebomen met diepere wortels. Onze resultaten wijzen op een beperking van bosbomen voor dispersie in open verbrande plaatsen (**hoofdstuk 5**).

Het samengestelde bewijs in dit proefschrift ondersteunt de hypothese dat in de Amazone bossen in overstromingsvlaktes minder veerkrachtig zijn, en een hogere kans hebben om teveranderen in een savannetoestand, dan bossen in hoogvlaktes. Het verminderde vermogen van overstromingsvlaktes om de bodemvruchtbaarheid te behouden en dat om de bosstructuur te herstellen na een brand kunnen de transitie naar savanne versnellen. Ik heb ook bewijs gevonden voor dispersielimitatie voor bosbomen uit overstromingsvlaktes. Analyses op brede schaal van bosbedekking als een functie van regenval suggereren dat savannes waarschijnlijk eerst in overstromingsvlaktes zullen uitbreiden als het klimaat in de Amazone droger wordt. Savanne-uitbreiding via ecosystemen in overstromingsvlaktes naar het hart van de Amazone kan kwetsbaarheid verspreiden vanuit een onverwachte plaats.

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Short biography

Bernardo Monteiro Flores was born in March 2nd 1983 in the city of Salvador, Brazil. At the age of two, he moved with his family to Rio de Janeiro. Between eight and ten, he lived with his parents and younger brother in England, for the MSc course of his father. In 2000, Bernardo graduated school at Colégio Santo Ignácio, Rio de Janeiro.

The next step was to study the BSc at the Federal University Fluminense. In 2006 Bernardo graduated in Marine Biology. His first scientific experience was to study behavioural responses of spinner dolphins in the oceanic Archipelago of Fernando de Noronha. Despite his passion for the ocean, only when he went deep into the Amazon forest in 2006 he discovered his study system. During his first year in the Amazon, Bernardo studied the effect of human disturbances in forest nutrient cycling at the National Institute for Amazonian Research (INPA). After observing for the first time the patterns of litter fall in mature and secondary forests, Bernardo fell in love with science and decided to do his MSc in Ecology at INPA in 2008. The topic of his MSc dissertation was the impact of fire on floodplain forests of the Negro river, developed with Bruce Nelson which whom Bernardo worked together for four years. This was the start of a new line of research, unknown for the scientific community. Floodplain forests are iconic Amazonian ecosystems, with their trees emerging from the river's black waters. The MSc study suggested that, compared to other tropical forests, these floodplain forests could be less resilient to drought and fire, indicating the path for his PhD.

Bernardo chose two institutions to develop this idea and study the resilience of Amazonian forests, the Federal University of Rio Grande do Norte, in Brazil, and Wageningen University in the Netherlands. His passion for science and his ideas for new studies are persistent, showing that this relationship is bound to be a long one.

For the next years, Bernardo will continue addressing the topic of forest resilience, trying to assess in detail the risk of savanna expansion in relation to climate change, and in collaboration with researchers in different parts of the world.

Publications

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Wageningen, 14 September 2016

the Chairman of the SENSE board

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The SENSE Research School declares that **Mr Bernardo Monteiro Flores** has successfully fulfilled all requirements of the Educational PhD Programme of SENSE with a work load of 49.3 EC, including the following activities:

SENSE PhD Courses

- Bayesian statistics (2014)
- Environmental research in context (2014)
- Research in context activity: Co-organising 3rd Wageningen PhD Symposium 'Diversity in science', Wageningen (2016)

Other PhD and Advanced MSc Courses

- Techniques for writing and presenting scientific papers, Wageningen University (2012)
- Population ecology, Federal University of Rio Grande do Norte (UFRN) (2012)
- Community ecology, Federal University of Rio Grande do Norte (UFRN) (2012)
- Biostatistics, Federal University of Rio Grande do Norte (UFRN) (2012)
- Conservation biology, Federal University of Rio Grande do Norte (UFRN) (2013)
- Summer school: Governing landscape restoration - governance, restoration, privatisation, Wageningen University (2015)

External training at a foreign research institute

- Training in field techniques of tree species identification, the implementation of field experiments in the Amazon forest, and conducting soil analyses, National Institute for Amazonian Research (INPA) (2013)

Management and Didactic Skills Training

- Teaching in the PhD capacitation programme in the BSc course: 'Community and Ecosystem Ecology', Federal University of Rio Grande do Norte (UFRN) (2012-2013)
- Supervising field work of MSc student with thesis entitled 'Regeneration of burned Amazonian Floodplain Forests' (2013)

Oral Presentations

- *Fire disturbance in Amazonian blackwater forests.* Annual Meeting of the Association for Tropical Biology and Conservation (ATBC), 19-22 June 2012, Bonito, Brazil
- *Blackwater floodplains and the resilience of Amazonian forests to fire.* European Annual Conference of Tropical Ecology, 7-10 April 2015, Zurich, Switzerland
- *Drought-driven fires and resilience of Amazonian floodplain forests.* Annual Meeting of the Association for Tropical Biology Conservation (ATBC), 18-23 June 2016, Montpellier, France

SENSE Coordinator PhD Education

Dr. ing. Monique Gulickx

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