

ALTERNATIVE PATHS OF SUCCESSION THROUGH SHRUB ENCROACHMENT IN AMAZONIAN FLOODPLAINS

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Abstract

Successional sequences from open sites to closed forests may take different pathways depending on the initially established vegetation. In Amazonian whitewater floodplains, we analysed encroachment by a monodominant shrub, the native fast-growing woody *Senna reticulata*. We analysed the impact of *S. reticulata* on woody plant diversity and the development of successional stages of deforested areas. The main hypothesis was that there is a difference in species abundance, diversity, composition and biomass between *S. reticulata* stands aged 2 and 6 years, and that with increasing stand age species abundance, diversity and biomass increase. We determined all woody plants in plots dominated by *S. reticulata*, two years and six years old. Our results showed that in the first two years *S. reticulata* is highly encroaching and forms almost monodominant stands by outshading other species including competing C4 grasses. Within six years the result was a positive balance for native species diversity where the re-establishment of the matrix vegetation was facilitated. This led to a similar vegetation composition and structure as is likely to install by typical successional sequences. With our data we could show that shrub encroachment does not necessarily lead to declines in ecosystem functions. Our study shows that the designation of encroachment as a process leading to functionally, structurally or contextually degraded ecosystems is not supported. On the contrary, it is a good example for recent statements that the commonly established link between shrub encroachment and degradation is not universal. The ecosystem was ecologically enhanced by encroachment as it facilitated the re-establishment of the matrix vegetation within less than a decade.

Key words: Shrub encroachment, floodplain forest, habitat change, ecosystem processes, succession, forest regeneration.

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Resumo

As sequências sucessionais de áreas abertas para florestas, podem tomar caminhos diferentes, dependendo do tipo de vegetação que inicialmente se estabelece. Nós analisamos a invasão de *Senna reticulata*, arbusto nativo monodominante de rápido crescimento em Várzeas Amazônicas. Analisamos o impacto de *S. reticulata* sobre a diversidade de plantas lenhosas e o desenvolvimento de estágios sucessionais de áreas desmatadas para formação de pastagens. Nossa hipótese prediz que existe uma diferença na abundância de espécies, diversidade, composição e biomassa entre estandes de *S. reticulata* de 2 e 6 anos de idade. Com o aumento da idade dos estandes aumenta a abundância, diversidade e biomassa. Nós amostramos todas as plantas lenhosas em parcelas de dois anos e seis anos de idade dominadas por *S. reticulata*. Nossos resultados mostraram que nos dois primeiros anos *S. reticulata* é altamente invasora, e forma estandes monodominantes, removendo outras espécies, inclusive as concorrentes gramíneas C4. Nas parcelas de seis anos, o resultado foi um saldo positivo para a diversidade de espécies nativas, onde o restabelecimento da vegetação matriz foi facilitado. Isto leva a uma composição e estrutura da vegetação semelhante à que era provável de instalar por sequências sucessionais típicas deste tipo de vegetação. Com os nossos dados, mostramos que a invasão pelo arbusto não leva necessariamente ao declínio das funções dos ecossistemas. Nosso estudo mostra que a denominação de invasão como um processo que conduz os ecossistemas à degradação das suas funções ou estrutura não é suportado. Pelo contrário, é um bom exemplo da não universalidade do vínculo estabelecido entre a invasão de arbustos e a degradação de ecossistemas. O ecossistema foi ecologicamente melhorado pela invasão, pois facilitou o restabelecimento da vegetação matriz em menos de uma década.

Palavras-chave: Invasão de arbusto, floresta de várzea, mudança de habitat, processos do ecossistema, sucessão, regeneração da floresta.

Introduction

Successional sequences from open sites to closed forests may take different pathways depending on the initially established vegetation. The vegetation matrix in Amazonian whitewater floodplains, so-called seasonal várzea (Prance, 1979), is highly diverse forest, the most species rich floodplains in the world (Wittmann et al., 2006; 2013). Flooding has a strong impact on the organisms inhabiting these floodplains, with durations up to 8 months per year and flood heights reaching 8m (Junk, 1989). The high regularity and predictability of the flooding periodicity enabled the vegetation to form adaptations to cope with the annual extreme hydric changes (Parolin et al., 2004). Only where flood durations exceed 240d/8m, trees will not establish and grasses and macrophytes dominate (Junk, 1989). Natural open sites frequently occur due to river dynamics and strong erosion and sedimentation in this highly dynamic ecosystem with sedimentation rates of up to one meter per year (Irion et al., 1997). A typical successional sequence beginning with fast-growing C4

grasses *Paspalum fasciculatum* Willd. over a phase dominated by *Salix martiana* Leyb. and *Cecropia* spp. and then a phase of *Pseudobombax munguba* (Mart.) Dugand leads back to the highly diverse forest matrix (Worbes et al., 1992). However, if the succession starts in man-made open grasslands in the floodplains, with high nutrient input due to presence of cattle, encroachment by the monodominant shrub *Senna reticulata* (Willd.) Irwin & Barn. (Caesalpiniaceae) (synonyms *Cassia alata* L., *Cassia reticulata* Willd.; Lorenzi, 1991) takes place. This is a native fast-growing woody plant which is locally called “pasture killer”. It grows to a maximum of 12 m height (Parolin, 1998; 2001) and colonizes open areas in nutrient rich Amazonian whitewater floodplains. It forms densely shrubby or forested stands along the river floodplains where people live (Figure 1). Its early growth is typical of encroaching species, i.e. an indigenous woody or shrubby plant which increases drastically in density, cover and biomass at the expense of other species (Van Auken, 2009).

In the natural successional sequence, C4 grasses and *Cecropia*-stands dominate and *Senna reticulata* has no importance. Only when there are big pastures with cattle and a high input of nutrients, the *S. reticulata* dominates with its very fast growth in height and density. Its fast establishment impedes the dominance of other early successional species (Parolin, 2001; 2005) or formerly established herbs. The local farmers whose predominant land use practice are small homegardens and livestock grazing, call the species “pasture killer” (matapasto; Figure 1A) and fight against its establishment by cutting, burning and flooding it. *S. reticulata* then dominates and fulfills all requirements to be defined as an encroaching species (Eldridge et al., 2011).

Shrub encroachment is defined as the increase in density, cover and biomass of indigenous woody or shrubby plants (Van Auken, 2009; Eldridge et al., 2011). Encroachment of woody vegetation into grasslands is a widespread phenomenon that alters plant community composition and ecosystem function (Wright et al., 2012). A dominance of the encroaching species initiates a plant succession which leads to the transformation of a grass-dominated to a tree-dominated ecosystem. This way, unmanaged grasslands become colonised by fast-growing light-demanding woody species and the herbaceous vegetation decreases in species number and biomass. By providing shade, the newly established encroaching species may be the starting point of a natural succession enabling shade-tolerant woody species to germinate and grow.

In general, ecological studies suggest that shrub encroachment is an ecological expression of degradation (Eldridge et al., 2011) with general reductions in ecosystem functions and processes (Van Auken, 2000; 2009; Archer, 2011). Such shrublands are considered as poorer than the diverse initial grasslands, causing reductions of plant biomass and species richness besides other effects on the vegetation (Zarovalli et al., 2007; Van Auken, 2009). However, Eldridge et al. (2011) recently stated that the commonly established link between shrub encroachment and degradation is not universal and that productivity, particularly reduced primary and secondary production, are not the necessary outcome of shrub encroachment.



Figure 1: Amazonian floodplains with A) *S. reticulata* flowering in its natural environment, B) highly diverse matrix floodplain forest in the high-water period, and C) natural grassland in the low-water period.

Shrub encroachment by *S. reticulata* leads to extremely dense monospecific stands in nutrient-rich Amazonian floodplains (Parolin, 2005). However, as the system is highly dynamic and very nutrient-rich, we postulate that it has a high resilience, where the matrix vegetation – the highly diverse *várzea* forests – re-establishes itself within rather short periods of time in less than a decade.

The aim of the present study was to determine the impact of encroachment by *S. reticulata* on plant diversity and the development of successional stages. We document the influence of this native but locally invasive species on woody plant diversity and on the regeneration in deforested areas. Forest is the matrix and the dominant vegetation form in Amazonian floodplains near the main river channels. Therefore, we focused our analyses on trees and shrubs. With the aim to determine the impact of encroachment by *S. reticulata*, we followed the hypothesis that woody plant encroachment by *S. reticulata* leads to significant declines in species richness (Ratajczak et al., 2012) but only for some years, and that thereafter the high diversity of the matrix forest is achieved. The hypothesis followed was that *S. reticulata* facilitates the establishment of highly diverse forests via encroachment showing differences in species abundance, diversity, composition and biomass between *S. reticulata* stands aged 2 and 6 years. Increasing stand age should result in increasing species abundance, diversity and biomass, and contrary to other hypotheses (e.g. Kesting et al., 2009), an initial shrub invasion by *S. reticulata* should not lead to enhanced habitat diversity but to a decreased diversity only in the first two years, and thereafter, according to the habitat heterogeneity hypothesis (MacArthur & Wilson, 1967), lead to high species diversity. In order to test the hypotheses, we inventoried all woody species in seven plots on former pastures which were abandoned and were then dominated by *S. reticulata*. Five plots were located in stands abandoned two years earlier, and two plots in stands of 6 years, on farmlands in the vicinity of the city of Manaus, Brazil.

Materials and methods

We screened different farmlands (“*fazendas*”) in the vicinity of Manaus, Brazil, for different successional stages of *S. reticulata* stands. The farmers indicated the sites and the history of cutting and burning to us, and we controlled by the analyses of annual increment rings in the wood of several trees of different species, which are naturally formed due to periodical flooding (Worbes, 1989). The age of the analyzed vegetation stands was determined as two years age (five plots in two “*fazendas*”) and six years age (two plots in two “*fazendas*”). The chosen study areas were all located in the floodplains of the Amazon (Solimões) River, near the confluence with the Rio Negro near the city of Manaus (03°15′S, 59°58′W).

The climate is hot and humid. Mean monthly temperature is 26.6°C (Ribeiro & Adis, 1984) and mean annual precipitation is about 2105 mm, with 75 % falling in the rainy season from December to May. The seasonality of

precipitation in the catchment area of the Amazon (Solimões) River results in an annual cycle of river discharge. Water levels near Manaus change with a mean amplitude of 8 m per year in the areas where trees grow.

Species were identified in the field with the help of José F. Ramos from INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus) and Leandro V. Ferreira (INPA/Smithsonian Institution, Manaus). Identifications were checked in the herbarium of the INPA.

All woody species including lianas with dbh > 1 cm or a height > 1 m were inventoried in the seven plots of 25 x 25 m each. For each tree, species, diameter at breast height (dbh), tree height, crown length and crown width were measured.

Results

The number of stems of *S. reticulata* differed in the plots of differing age, with an abundance of 1339 individuals, which corresponds to a relative density of 86.4%, in the 2y-old plots vs. 198 individuals making 28.4% relative density in the 6y old stands. Relative frequency in the plots was 100% in both age groups as the main criteria for choosing a site was the presence of *S. reticulata* in the plots. Basing on the dbh, which in both plot ages was 5 cm, calculated absolute dominance of the trees of this species was 1.3 m²/ha (2y) vs. 0.2 m²/ha (6y). This results in a relative dominance of 93.7% (2y) vs. 52.9% (6y).

The total number of species in the plots of 2y was 32, with 7-22 species per plot (Annex 1). In the 6y old plots, total number of species was 34, with 24 and 30 species per plot (Annex 2).

There was a clear separation between the 2- and the 6-year old plots, as shown by cluster ordination (Figure 2) and PcoA ordination (Figure 3, Table 1). The 2-year old plots were split depending on the “fazenda” where the inventory was performed.

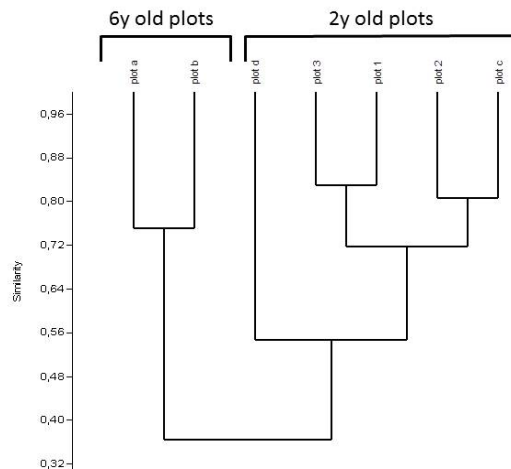


Figure 2: Cluster ordination of the plots of succession vegetation in Central Amazonian floodplains. Coefficient 0.9298; Min Y= 0,3019; Algorithm= paired group; similarity measure= Bray-Curtis.

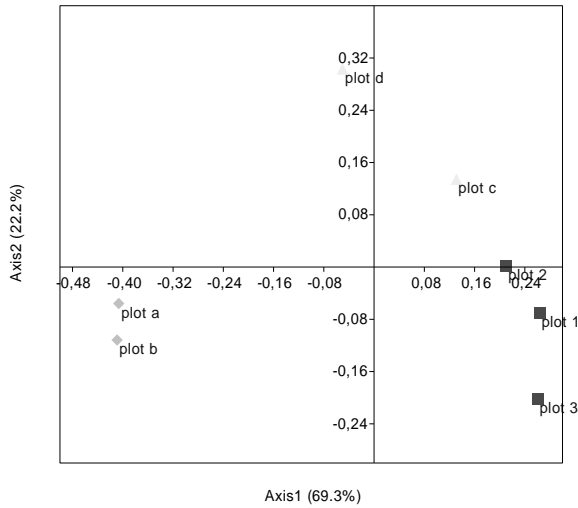


Figure 3: PcoA ordination of the analysed plots of succession vegetation in Central Amazonian floodplains. Coefficient 0.9298; Min Y= 0,3019; Algorithm= paired group; similarity measure= Bray-Curtis.

Table 1: PcoA ordination of the analysed plots with stands of *Senna reticulata* of differing age on two "fazendas".

PCoA_results	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
plot 1	0,33762	-0,15473	-0,38153	0,071839	-0,04665	0,00165
plot 2	0,38407	-0,08791	0,2482	-0,04184	-0,18709	0,008833
plot 3	0,40888	0,008561	0,12695	0,013627	0,22856	-0,012
plot c	-0,31538	-0,32471	-0,04743	-0,28264	0,031148	0,00373
plot d	-0,43262	-0,35968	0,095494	0,23642	0,003615	-0,01262
plot a	-0,19546	0,43743	-0,01596	0,015176	-0,00055	0,1651
plot b	-0,18711	0,48104	-0,02572	-0,01259	-0,02904	-0,15469
Eigenvalue	0,53392	0,1712	0,03068	0,022685	0,010376	0,001649
Percent	69,294	22,219	3,9817	2,9441	1,3467	0,21404

Discussion

Senna reticulata was a good initiator of natural forest stands, the first step to successional sequences which can replace *Cecropia* monodominant stands with the same long-term outcome, forming species rich floodplain forests which are adapted to frequent disturbances. Grasses were not present because of the encroachment which hinders the establishment of light-demanding species. This may be a positive characteristic as the natural vegetation in sites flooded for up to 210 days a year in Central Amazonian floodplains is forest and not open grasslands or savannas (Junk, 1989). Therefore abandoned pastures recover to forest within 10-20 years also through the presence of *S. reticulata* who – despite of encroachment and outcompeting of other species for some years – on the long run leads to a diverse forest (Figure 4).

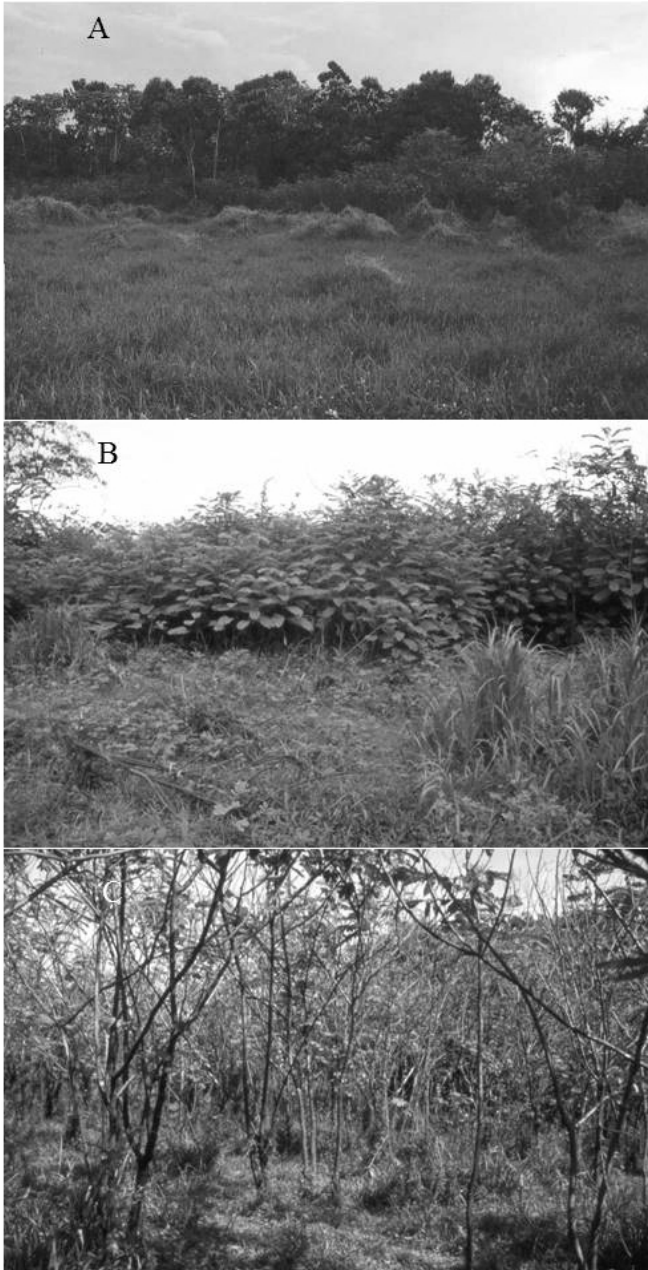


Figure 4: Different phases of the encroachment with *S. reticulata* in Amazonian floodplains. A) natural pasture without *S. reticulata*, B) site of two years age, C) site of six years age after abandonment.

Encroachment vs succession delimitation of terms, temporal aspect - in tropical rainforest biome fast evolution of the vegetation, thus fast development from phase of encroachment with monodominant stands of local non alien species, but then after few years is initial phase to succession back to matrix forest just as the "natural" non-encroaching pathway (Figure 5). Normal succession takes a different pathway than the one by encroachment with *S. reticulata*, but, after only a few years, the two different pathways reach the same result, the highly diverse várzea forest (Figure 5). The final species composition of the *Senna*-dominated plots of 6y age and the matrix forest as described by Worbes et al. (1992) can be expected to be rather similar as the species composition of the old encroached sites are already similar in the composition of species to what is described as typical várzea forest in the region (Worbes et al., 1992; Wittmann et al., 2006).

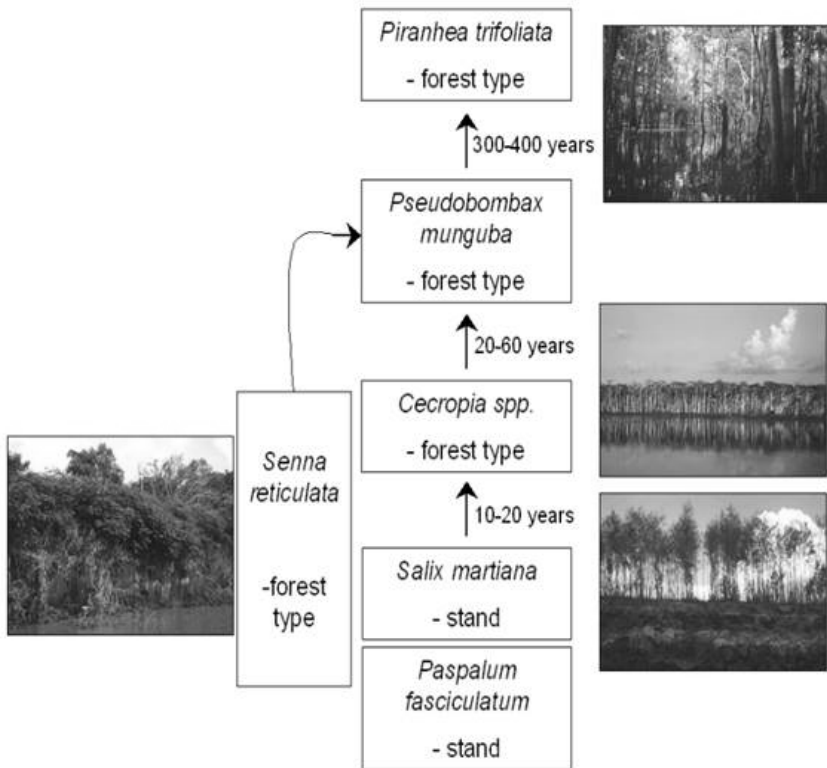


Figure 5: Pathways of succession in Central Amazonian floodplain forest, with the natural successional sequence as described by Worbes et al. (1992), and the alternative pathway via the encroaching phase dominated by *Senna reticulata*. Scheme of natural succession and encroachment by *Senna reticulata*. Adapted from Parolin 2005.

Our results highlight that *S. reticulata* is a species which, despite being locally invasive and highly encroaching, leads to a positive balance for native

species diversity and initiates the re-establishment of the matrix vegetation within only 1-2 decades. This is in line with Eldridge et al. (2011) who stated that shrub encroachment does not necessarily lead to declines in ecosystem functions. Our study shows that the simple designation of encroachment as a process leading to functionally, structurally or contextually degraded ecosystems is not supported (Eldridge et al., 2011).

Our study also shows that encroachment is not common only in the world's arid and semiarid biomes, where it is the focus of many studies in the past decade (Eldridge et al., 2011; 2012; Alofs & Fowler, 2013). A nutrient-rich wetland environment can be just as affected by an encroaching species, only that the system is more dynamic, and developments of vegetation change back to the matrix are much faster than in systems where water and nutrients are clearly limiting.

The limiting force in our ecosystem is the long duration of flooding by a high water column, a constraint which usually is lethal for trees (Larcher, 1994). However, due to the very long existence of dynamic floodplains along the main rivers of the Amazon basin (Junk, 1997), the number of adapted species is extraordinarily high and the constraints imposed by waterlogging and submergence do not affect plant development to a critical degree. *S. reticulata* displays mechanisms that prevent the plants from decreasing their biomass under waterlogged conditions (Arenque et al., 2014). Starch accumulation during the terrestrial phase provides carbohydrate resources for biomass production even despite unfavourable growth conditions, which makes this species highly competitive.

Much more critical is drought, which affects *S. reticulata* and many other species (Parolin et al., 2010) and which may have serious influences on vegetation distribution and successional sequences especially in the light of increasing events of long-term drought which are to be expected in the next decades in the Amazon basin (Cox et al., 2008). Like most species from Amazonian floodplains, *S. reticulata* can grow in non-flooded uplands (pers. observ.) but apparently it is not competitive enough there. We never observed huge stands far from water. Other spp like e.g. *Vismia* (Mesquita et al., 2001) dominate the corresponding sites in the nutrient-poor uplands.

In this context we found evidence that the shrub's traits influence the functional outcome of encroachment (Eldridge et al., 2011). Being highly tolerant against extreme waterlogging due of its morphological adaptations and very high growth performance (Parolin, 2001; 2005; Arenque et al., 2014), *S. reticulata* can outcompete other species which could otherwise profit from the abandoned open sites. No other invasive species has been observed to play an important role in Amazonian floodplains, especially no true alien species. Due to the extreme flooding tolerance the species involved do not suffer from competition from other species because the periodical flooding of up to 8m height for up to 240 days per year is such a strong selective factor that only the highly adapted species can survive and grow vigorously (Parolin, 2013).

The occurrence of single trees of *S. reticulata* is rarely observed. Very dense populations on the other hand occur in heavily impacted areas with high

nutrient input. This is congruent with the finding that encroachment appears to result from distinct factors including overgrazing and recovery from anthropogenic disturbance (Scholes & Archer, 1997; Eldridge et al., 2011). *S. reticulata* forms these stands only on highly disturbed formerly cleared sites. The densest stands are found only where human action created a perfect environment for this species: open grasslands with very high light incidence, no competition from herbaceous species due to grazing (cattle do not like *S. reticulata* particularly) and much nutrient input by the cattle.

A reason why this species is so efficient in cattle pastures is linked to the particularly high availability of nutrients, which enables this one plant species to grow up to 4m in the first year and outshade all competitors with its extremely dense canopy (Parolin et al., 2004). There also might be an importance in the role of the dispersal syndrome of the encroaching species, which is highly efficient in wind and water dispersal (Parolin et al., 2013) as are most encroacher species (Eldridge et al., 2011).

However, human land use practices lead to a decrease of forest cover and of species diversity through deforestation for timber use, and for cattle ranching. Ecological changes are easily observed due to the conversion of forests into pastures, which are mostly dominated by the artificially installed *Brachiaria* spp. causing drastic changes to the natural species composition (Parolin, 2005).

An increasing body of evidence suggests that shrubs play an important ecological role by providing habitat for understory plants, particularly linked to overgrazed and degraded rangeland (Eldridge et al., 2011), which however is not the case in central Amazonian floodplains. The role of *S. reticulata* in facilitating understory growth was shown in our study. The large canopies supported more species which established after only few years. Our study demonstrates that this one species of woody shrubs facilitated the establishment of a big number of species already after 2 years, and after 6 years these were present in all analysed plots.

Bush encroachment has serious economic implications on agriculture (Karuaera, 2011). It results in the decline of livestock production due to the loss of grass production on the grazing lands. It also results in lower productivity of individual animals as most encroaching woody species are inedible to domestic livestock (Wiegand et al., 2005).

Conclusions

An example for facilitation of woody plant establishment via encroaching in a stressful environment is presented. Encroachment may lead to many outcomes ranging from desertification to ecosystem enhancement (Eldridge et al., 2011). The overall negative view of the effects of shrub encroachment has been strongly influenced by the prevalence of land use and is linked to ecosystems which lack water and nutrients, such as semi-deserts. Both these resources, water and nutrients, are available in exceeding quantities in Amazonian floodplains.

Our data support the statement that an ecosystem may return to its initial forested state by encroachment as it enables the fast re-establishment of the matrix vegetation. This is not achieved when fast-growing C4 grasses dominate, such as typically *Paspalum fasciculatum* Willd. and *Echinochloa polystachya* (Kunth) Hitchc. (Piedade et al., 1991), considered the world's most productive grasses. Once established, it is difficult for woody species to invade these areas. Only *S. reticulata* is capable of this and initiates the succession towards the diverse forest matrix. This desirable development from an ecological and conservationist perspective however is not necessarily a positive outcome for the local farmers whose intention is the maintenance of an open grassland for the purpose of cattle ranching. In Amazonian floodplains like in other ecosystems, bush encroachment has adverse effects on livestock farming and results in the decline of livestock production, due to the loss of grass production on grazing lands. Therefore, planting this species would not be advantageous for the owners of farmlands but could enable the regrowth of highly diverse floodplain forests.

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Annex 1: Tree species in plots aged 2 years on two “fazendas” in Central Amazonia, with species and family as well as local name and number of stems in each plot.

species	family	local name	plot 1	plot 2	plot 3	plot c	plot d
<i>Senna reticulata</i>	Caesalpiniaceae	Matapasto	333	256	406	217	127
<i>Triplaris surinamensis</i>	Polygonaceae	Tachí	1	6	5	1	0
<i>Vitex cymosa</i>	Verbenaceae	Taruma	3	8	11	0	0
<i>Zanthoxylum compactum</i>	Rutaceae	Limorana	8	2	19	0	0
<i>Crateva benthami</i>	Capparidaceae	Catoré	10	5	7	0	0
<i>Ocotea amara</i>	Lauraceae	Louro	3	3	4	3	1
<i>Cecropia latiloba</i>	Cecropiaceae	Imbauba branca	0	1	0	2	1
<i>Genipa americana</i>	Rubiaceae	Genipapo	0	3	4	0	0
<i>Tabebuia barbata</i>	Bignoniaceae	Capitari	0	2	11	0	0
<i>Platymiscium ulei</i>	Papilionaceae	Macacaúba	0	0	0	5	1
<i>Pseudobombax munguba</i>	Bombacaceae	Munguba	9	1	1	0	0
<i>Astrocaryum jauari</i>	Arecaceae	Jauari	0	3	5	0	0
<i>Ficus anthelmintica</i>	Moraceae	Caxinguba	0	3	4	0	0
<i>Cecropia membranacea</i>	Cecropiaceae	Imbauba amarela	0	0	0	1	3
<i>Solanum critino</i>	Solanaceae	Jurubeba	0	0	0	1	5
<i>Erythrina fusca</i>	Papilionaceae	Mulungú	0	0	0	2	3
<i>Macrolobium acaciifolium</i>	Caesalpiniaceae	Arapari	1	3	0	0	0
<i>Campsiandra angustifolia</i>	Caesalpiniaceae	Acapurana	0	1	3	0	0
<i>Cassia leiandra</i>	Caesalpiniaceae	Marimari	0	2	1	0	0
<i>undet. Legum.</i>	Leguminosae	Agudaoeira	0	1	2	0	0
<i>Inga punctata</i>	Mimosaceae	Ingá	0	0	1	1	0
<i>Entata polyphylla</i>	Mimosaceae	Paricarana	0	1	1	0	0

<i>Xylosoma intermedium</i>	Flacourtiaceae	Limorana 3	0	7	0	0	0
<i>Bauhinia sp.</i>	Caesalpiniaceae	Pé de vaca *	0	5	0	0	0
<i>Buchenavia oxycarpa</i>	Combretaceae	Tanibuco	0	0	2	0	0
<i>Ormosia sp.</i>	Fabaceae	Buiussu	0	0	0	1	0
<i>Laetia corymbulosa</i>	Flacourtiaceae	Sardinheira	0	0	1	0	0
<i>Inga sp. 1</i>	Mimosaceae	Ingá-açu	0	0	1	0	0
<i>Sapium glandulosum</i>	Euphorbiaceae	Tapuru	0	0	0	1	0
<i>Arrabidaea sp.</i>	Bignoniaceae	Unha de cigana *	0	1	0	0	0
<i>Piranhea trifoliata</i>	Euphorbiaceae	Piranheira	0	1	0	0	0
<i>Zygia inaequale</i>	Mimosaceae	Zygia	0	1	0	0	0

Annex 2: Tree species in plots aged 6 years on two “fazendas” in Central Amazonia, with species and family as well as local name and number of stems in each plot.

	Species	Family	Local name	Plot a	Plot b
1	<i>Senna reticulata</i>	Caesalpiniaceae	Matapasto	94	104
2	<i>Platymiscium ulei</i>	Papilionaceae	Macacaúba	82	150
3	<i>Ocotea amara</i>	Lauraceae	Louro	29	33
4	<i>Genipa americana</i>	Rubiaceae	Genipapo	2	11
5	<i>Astrocaryum jauari</i>	Arecaceae	Jauarí	7	3
6	<i>Erythrina fusca</i>	Papilionaceae	Mulungú	18	8
7	<i>Ormosia sp.</i>	Fabaceae	Buiussu	1	15
8	<i>Cecropia latiloba</i>	Cecropiaceae	Imbauba branca	10	4
9	<i>Zanthoxylum compactum</i>	Rutaceae	Limorana	7	9
10	<i>Ouratea sp.</i>	Ochnaceae	Canicero	6	6
11	<i>Sapium glandulosum</i>	Euphorbiaceae	Tapuru	3	8
12	<i>Inga punctata</i>	Mimosaceae	Ingá	4	4
13	<i>Campsandra angustifolia</i>	Caesalpiniaceae	Acapurana	4	5
14	<i>Arrabidaea sp.</i>	Bignoniaceae	Unha de cigana *	4	4
15	<i>Salacia sp.</i>	Hippocrataceae	Cipó *	4	3
16	<i>Triplaris surinamensis</i>	Polygonaceae	Tachí	1	4
17	<i>Cecropia membranacea</i>	Cecropiaceae	Imbauba amarela	3	3
18	<i>Zanthoxylum sp.</i>	Rutaceae	Limorana 2	2	3
19	<i>Solanum critino</i>	Solanaceae	Jurubeba	4	1
20	<i>Pseudobombax munguba</i>	Bombacaceae	Munguba	2	1
21	<i>Pouteria glomerata</i>	Sapotaceae	Abiurana	6	0
22	undet. Legum.	Leguminosae	Agudaoeira	5	0
23	<i>Laetia corymbulosa</i>	Flacourtiaceae	Sardinheira	4	0
24	<i>Casearia aculeata</i>	Flacourtiaceae	Patajuba	2	0
25	<i>Schizolobium sp.</i>	Caesalpiniaceae	Paricarana 2	2	0
26	<i>Psidium acutangulum</i>	Myrtaceae	Goiaba arça	2	0
27	<i>Pseudoxandra polyphleba</i>	Annonaceae	Envira	0	2
28	<i>Ilex inundata</i>	Aquifoliaceae	Turima	0	2
29	<i>Eugenia sp.</i>	Myrtaceae	Goiabarana	1	0
30	<i>Fagara compactum</i>	Rutaceae	Tamaqueira	0	1
31	<i>Entata polyphylla</i>	Mimosaceae	Paricarana	1	0
32	<i>Spondias lutea</i>	Anacardiaceae	Taperebá	1	0
33	<i>Xylosoma intermedium</i>	Flacourtiaceae	Limorana 3	1	0
34	<i>Inga sp.</i>	Mimosaceae	Ingá-açu	0	1