

ORIGINAL ARTICLE

Conservation potential of shade-tolerant forest species in agricultural mosaics in the eastern Brazilian Amazon

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ABSTRACT

Shade-tolerant forest species are among the most susceptible to habitat loss in agricultural mosaics, where a variety of croplands is connected to forests at different levels of anthropogenic disturbance. We aimed to evaluate the community similarity of shade-tolerant species among different land use types across agricultural mosaics with different levels of disturbance. The study was conducted in three municipalities in southern and southeastern Pará state, in eastern Amazonia. A multiple-community similarity measure based on the Horn similarity index was used to compare land use types and assess the resilience of shade-tolerant species towards forest loss and disturbance at the landscape level. High shade-tolerant species similarity was found between mature forest fragments that underwent different levels of disturbance in all three agricultural mosaics, but secondary forests had lower similarity with mature forest in the most fragmented and altered mosaic. Shade-tolerant species showed very low density in croplands, but the same group of species seemed to colonize agricultural fields of annual crops and clean pasture, as they showed high community similarity. Another group of species was present in invaded pastures, probably due to the effects of time since land abandonment after woody species colonization. Mixed tree plantations were more similar to mature and secondary forests than other types of croplands. Shade-tolerant species similarity was higher among land use types inserted in agricultural landscapes that maintained conserved forest fragments. Our results suggest that the conservation of mature forests and landscape connectivity are crucial to the maintenance of shade-tolerant species in agricultural mosaics.

KEYWORDS: floristics; land use; pasture; resilience; similarity

Potencial de conservação de espécies tolerantes à sombra em mosaicos agrícolas na Amazônia Oriental Brasileira

RESUMO

As espécies florestais tolerantes à sombra estão entre as mais suscetíveis à perda de habitat em mosaicos agrícolas, onde uma variedade de terras agrícolas está conectada a florestas em diferentes níveis de distúrbio antropogênico. Este trabalho teve como objetivo avaliar a similaridade da comunidade de espécies tolerantes à sombra entre diferentes tipos de uso da terra em mosaicos agrícolas com diferentes níveis de perturbação. O estudo foi realizado em três municípios localizados no sul e sudeste do estado do Pará. Uma medida de similaridade de comunidade múltipla baseada no índice de similaridade de Horn foi usada para comparar diferentes tipos de uso da terra em três diferentes mosaicos. Alta similaridade de espécies tolerantes à sombra foi encontrada entre fragmentos de florestas maduras que sofreram diferentes níveis de distúrbio nos três mosaicos agrícolas, mas florestas secundárias apresentaram menor semelhança com a floresta madura no mosaico mais fragmentado e alterado. As espécies tolerantes à sombra apresentaram densidades muito baixas nas terras agrícolas, no entanto, o mesmo grupo de espécies tolerantes à sombra parece colonizar os cultivos anuais e as pastagens limpas. Por outro lado, outro grupo de espécies esteve presente em pastagens invadidas. As plantações mistas de árvores foram mais semelhantes às florestas maduras e secundárias do que outros tipos de terras agrícolas. Nossos resultados sugerem que a conservação de florestas maduras e da conectividade da paisagem são cruciais para a manutenção de espécies tolerantes à sombra em mosaicos agrícolas.

PALAVRAS-CHAVE: florística; pastagem; resiliência; similaridade; uso da terra

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INTRODUCTION

Land use change has been considered as the main cause of global biodiversity loss (Newbold *et al.* 2015; Barlow *et al.* 2016). Many of the remaining forest fragments are embedded in landscapes that contain different types of land use, forming an agricultural mosaic, where a variety of croplands is connected to forests at different levels of anthropogenic disturbance (Do Vale *et al.* 2018).

In these agricultural mosaics, shade-tolerant forest species are most susceptible to natural and anthropogenic forest disturbances. These species have seeds that can germinate and establish in the forest understory (Swaine and Whitmore 1988). Their young individuals are thus commonly found beneath the forest canopy, but can occasionally be seen in open areas (Mitja *et al.* 2008), while adults can also be seen in agricultural fields, usually as remnants of the forests (Santos and Mitja 2011).

Open environmental conditions, competition with pioneer herbaceous species, absence of animals that disperse seeds, and disturbances during soil preparation for planting crops contribute to the loss of shade-tolerant species (Hooper *et al.* 2005; Esquivel *et al.* 2008). This species impoverishment in agricultural mosaics can result in profound consequences for forest restoration, such as erosion of diversity and shifts in the functional composition of forests in anthropogenic landscapes, and provision of forest ecosystem services (Da Silva and Tabarelli 2000; Van Breugel *et al.* 2013).

An approach to determine the conservation potential of shade-tolerant forest species in agricultural mosaics is the use of measures of species similarity as tools for describing changes in species composition along environmental gradients (Jost *et al.* 2011). In this sense, land use types can be compared to assess the resilience of shade-tolerant species towards forest loss and disturbance at the landscape level. The similarity between mature forests and forests that have undergone different levels of human disturbance reveals the conservation capacity of these habitats. On one hand, high similarity between mature forests and secondary forests indicates a successional process in the latter towards a greater dominance of late shade-tolerant species. On the other hand, high similarity between secondary forests and agricultural crops can be perceived as a delay in the floristic change over processes that are intrinsic to the forest succession (Do Vale *et al.* 2018).

Finally, although croplands may be different regarding the species that were planted and land preparation, or even land in degradation stage (e.g., clean and invaded pastures), high similarity of shade-tolerant species between croplands may indicate that these environments are a favorable habitat for a group of late succession species that can survive in open areas. This work aimed to evaluate the community similarity of shade-tolerant species among different land-use types across agricultural mosaics with different levels of disturbance. We

hypothesized that highly fragmented landscapes, with lower forest cover, present less similarity in shade-tolerant species between land-use types due to limitation in forest propagule dispersion. Additionally, we evaluated which shade-tolerant forest species were the most resilient to forest habitat loss within agricultural mosaics.

MATERIAL AND METHODS

Study Area

The study was conducted in 2008 at three rural communities with small family farms in the settlements of Palmares II, Maçaranduba and Travessão 338S, located in the municipalities of Parauapebas, Nova Ipixuna and Pacajá, respectively (Figure 1). Each community was considered as an agricultural mosaic where forest fragments are adjacent to different plantations. The communities are located in southern and southeastern Pará State, in the eastern Brazilian Amazon, in the region known as the Arc of Deforestation, where loss of biodiversity is intense, driven by changes in land use caused by deforestation for agriculture (Fearnside 2017). In addition, anthropogenic fires and severe drought events in the last decade also drive floristic and structural changes in the region and contribute to deforestation itself (Morandi *et al.* 2016).

The dominant primary vegetation is tropical rain forest, and the average annual temperature in the study area is approximately 26 °C. The climate is classified as super humid in Parauapebas, humid tropical in Pacajá and rainy tropical in Nova Ipixuna, according to the Köppen classification.

The Palmares II Settlement Project (05°51'22.2"–05°56'27.4"S, 49°52'06"–50°03'57.4"W) was established in 1996 with farms of average 86 ha (Figure 1). The settlement is the most fragmented of the three agricultural landscapes, with many pastures and croplands, in addition to the occurrence of recent ground fires in remaining forest areas. In Palmares II, unlike in the other two communities, farmers live in a village about 25 km distant from the agricultural fields, so more access roads and trails were opened, which helps to explain the greater degree of human impact on this area compared to the other two (Oszwald *et al.* 2011).

The community of Maçaranduba (04°45'45.1"–04°48'50.1"S, 49°19'13"–49°22'50.2"W) is located in the Praia Alta-Piranheiras Agricultural-Extractivist Settlement Project (Figure 1). This community was established in 1994 and farms average 71 ha. The landscape had a notably marked dynamic between 1997 and 2004, when 60% of changes in land use types occurred. The landscape mosaic is composed of pastures at different stages of evolution. The only surviving forest areas are secondary forests formed after cropland abandonment (more than 10 years old), riparian forest or forest fragments in areas of difficult access (Oszwald *et al.* 2011).

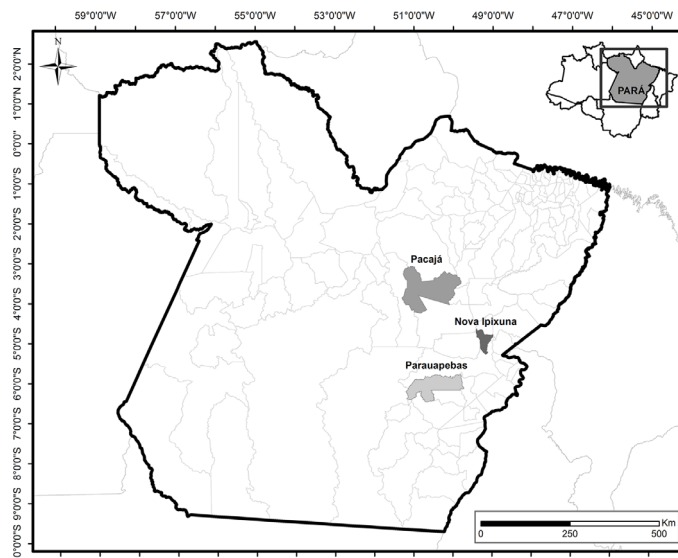


Figure 1. Location of the municipalities Parauapebas, Nova Ipixuna and Pacajá, in the State of Pará, in the eastern Brazilian Amazon, where the three agricultural mosaics were inventoried in the communities of Palmares II, Maçaranduba and Travessão 338S, respectively. The inset shows the position of Pará in northern Brazil.

The community of Travessão 338S (03°41'52"–03°46'48"S, 51°02'04.7"–51°03'28"W) is located along the Trans-Amazonian Highway (Figure 1). It was established in 2001 with farms of 26 ha. This area was the most recently affected by deforestation, and is still largely covered by a matrix of primary forest and large forest patches (Oszwald *et al.* 2011).

Sampling design

A socio-economic survey carried out with 50 small family farmers helped define which farms were most representative of each agricultural mosaic (De Sartre 2011). Nine representative farms were selected within each mosaic. Five sampling points were established at each farm for the inventory of vegetation, resulting in 45 sampling points per mosaic. The points were equally spaced along the longest diagonal of the farm, thus the distance between the points varied according to the farm size (from about 200 to 400 m). Because the points were systematically spaced along the diagonal of each farm, they were not selected based on the type of land use. Thus, it was assumed that the vegetation cover at each sampling point reflected the land use types prevailing in each mosaic, which resulted in a heterogeneous number of sampling points per land use type for each mosaic (Table 1).

Nine types of land use were identified in the three studied agricultural mosaics. The Palmares II mosaic is the only one that has mature burned forest, does not have mature conserved forest and has the largest number of annual crops. Maçaranduba has the largest area of pastures, while Travessão 338S has the largest area of mature forest and is the only one with mixed tree plantations (Table 1).

At each sampling point, the vegetation was sampled across three strata. A plot of 10 × 50 m (500 m²) was established for

the upper stratum inventory, composed by individuals with diameter at breast height (DBH) ≥ 10 cm. A subplot of 5 × 50 m was established for the middle stratum, composed by individuals with DBH < 10 cm and height ≥ 2 m. Finally, 10 subplots of 1 × 1 m were regularly distributed in the center of the plot for the lower stratum inventory, composed by individuals with 2 m > height ≥ 10 cm.

The species were classified into groups based on their life form (herb, liana, shrub, palm or tree), and their shade tolerance guild (pioneer or shade-tolerant) according to Mitja *et al.* (2008). Previous species identification was performed by a parataxonomist and was confirmed by comparison with specimens in the Herbarium João Murça Pires at the Museum Paraense Emilio Goeldi. The plants were classified in accordance with the Angiosperm Phylogeny Group III system. The few unidentified individuals (2, 5 and 6% of the individuals from Palmares II, Maçaranduba and Travessão 338S, respectively) were excluded from the analysis.

Statistical analysis

In order to highlight the forest species that survive in the different land use types at agricultural mosaics, floristic analysis was carried out using only the floristic composition of the shade-tolerant species, in which the pioneer species were excluded.

A multiple-community similarity measure based on the Horn similarity index (Horn 1966), modified according to Chao *et al.* (2008), was used to determine the floristic similarity between land use types within each mosaic. The Horn index weighs species by their abundance, which is more appropriate when rare species are important, as in conservation applications (Jost *et al.* 2011). To calculate the Horn index,

Table 1. Number of sampling points per land-use type in three agricultural mosaics (PII = Palmares II, M = Maçaranduba, T338S = Travessão 338S) studied in the “Arc of Deforestation” region, Pará state, Brazil.

Acronym	Land-use type	Description	Agricultural mosaics			Total
			PII	MAÇ	T338	
ConFor	Mature conserved forests	Forests with a well-defined vertical structure and no signs of recent human disturbance. (three vertical strata)	-	8	7	15
ExpFor	Mature exploited forests	Forests showing signs of disturbance, such as clearings resulting from timber extraction. (three vertical strata)	5	3	16	24
BunrFor	Mature burned forests	Forests showing signs of fire. (three vertical strata)	10	-	-	10
OldSec	Old secondary forest	Secondary forests with a defined woody upper canopy, older than 12 years. (three vertical strata)	3	9	4	16
YoungSec	Young secondary forest	Secondary forests lacking a defined upper woody stratum, younger than 12 years old. (two vertical strata)	6	4	5	15
InvPas	Invaded pastures ^a	Pastures with a high abundance of herbaceous individuals and young seedlings of woody species. (two vertical strata)	4	11	6	21
ClePas	Clean pastures ^a	Pastures with a low density of woody species. (two vertical strata)	7	9	1	17
AnnCrop	Annual crops	Rice (<i>Oryza</i> sp.), bean (<i>Vigna</i> sp.), corn (<i>Zea mays</i>) and especially cassava (<i>Manihot esculenta</i>) plantations. (two vertical strata)	10	1	2	13
MixTree	Mixed tree plantation ^b	Cocoa (<i>Theobroma cacao</i>) plantations generally combined with paricá (<i>Schizolobium amazonicum</i>) (two vertical strata)	-	-	4	4
Total sampling points			45	45	45	135

^a *Urochloa brizantha* was the predominant forage plant in Maçaranduba and Palmares II, while *Urochloa decumbens* predominated in Travessão 338S.

^b Mixed tree plantations are uncommon in southeastern Pará and were restricted to Travessão 338S, which is part of the cocoa-producing region in southern Pará

we first extrapolated the abundance of each species in the lower and medium stratum to the larger area of the upper stratum (500 m²) in order to standardize abundance among strata by plot, and divided the abundance by the number of sampling points on each land use type (Table 1). Finally, we summed the abundance of the three strata to eliminate the stratification at each sampling point. The mean abundance of the sampling points of each land use type was used to calculate the Horn index. Horn index (h) varies from 0 to 1, for minimum and maximum similarity, respectively. To compare the community similarity among land-use types, the index values were categorized in very low similarity ($h < 0.2$), low similarity ($0.2 \leq h < 0.4$), medium similarity ($0.4 \leq h < 0.6$), high similarity ($0.6 \leq h < 0.8$) and very high similarity ($h \geq 0.8$). Analyses were performed with the R-Studio interface for R Core Team (2019) using the SimilarityMult function of the SpadeR package, which compares the similarity between more than two communities (land use types) simultaneously, considering the species shared by all the communities.

RESULTS

In total, we found 1298 species across all mosaics and land use types, of which 968 were classified as shade-tolerant. Forests generally showed a higher total number of species, as well as a higher relative richness and relative abundance of shade-tolerant species when compared to croplands (Table 2). The land use types where we found highest proportions

of shade-tolerant species were exploited forests at Palmares II and conserved forests at Maçaranduba (84% of the species and 90 % of the individuals) and Travessão 338 (89% of the species and 95% of the individuals). Even though some croplands showed a relatively high total frequency of shade-tolerant species per plot (e.g., annual crops in Palmares II – 57%; mixed tree plantations in Travessão 338 – 56%), the total relative abundance of shade-tolerant species per plot was low, varying from 4% in clean pastures at Maçaranduba to 48% in mixed tree plantations at Travessão 338. Most of the individuals in those cropland types belonged to non-shade tolerant species (Table 2).

No case of very high similarity between land use types was recorded, and only four cases of high similarity were observed (Figure 2). At Palmares II, the predominance was of low or very low similarity among the types of uses, except between exploited and burned forests ($h = 0.6$), clean pastures and annual crops ($h = 0.71$), and annual crop and young secondary forest ($h = 0.53$) (Figure 2). At Maçaranduba only mature forests showed high similarity ($h = 0.64$), old and young secondary forests showed medium similarity with conserved and exploited forest, and clean and invaded pastures showed low or very low similarity with all other uses (Figure 2). At Travessão 338S, as in the other mosaics, only mature forests showed high similarity ($h = 0.72$), old secondary forests and mixed tree plantation showed medium similarity with mature

Table 2. Number of species per land-use type in three agricultural mosaics in the “Arc of Deforestation” region, Pará state, Brazil. Values are the average, standard deviation (SD), minimum (Min) and maximum (Max) number of species per plot, total (Total) number of species per land-use type and overall percentage of shade-tolerant species and individuals.

	Average	SD	Min	Max	Total	Total % shade-tolerant species	Total % shade-tolerant individuals
<i>Palmares II</i>							
Exploited forest	60	13	42	78	229	84	90
Burned Forest	47	19	17	84	303	78	70
Old secondary forest	27	7	19	32	87	64	41
Young secondary forest	23	11	11	35	154	56	37
Annual Crop	15	3	10	20	156	57	33
Invaded pastures	19	8	9	29	111	53	18
Clean pastures	25	23	9	59	78	45	15
<i>Maçaranduba</i>							
Conserved forest	59	10	43	72	272	86	92
Exploited forest	67	7	59	72	170	87	88
Old secondary forest	44	18	16	70	298	79	75
Young secondary forest	21	12	3	28	121	60	52
Invaded pastures	7	5	0	16	143	47	12
Clean pastures	3	2	1	6	74	28	4
<i>Travessão 338</i>							
Conserved forest	58	10	50	78	255	89	95
Exploited forest	60	38	36	228	446	87	93
Old secondary forest	49	10	36	58	176	87	94
Young secondary forest	28	5	22	33	147	72	42
Mixed tree plantation	22	7	13	30	130	56	48
Invaded pastures	7	7	1	18	69	48	7

forests, and the invaded pastures showed low or very low similarity with all others uses (Figure 2).

Shade-tolerant forest trees and palms represented a very low percentage of the relative abundance in croplands, with no species higher than 0.5%. *Attalea speciosa* Mart. ex Spreng. (0.49%), *Geissospermum vellosii* Allemão (0.12%), *Annona exsucca* DC. (0.35%) and *Tabernaemontana macrocalyx* Müll. Arg. (0.14%) showed higher relative abundance in mixed tree plantations, annual crops, invaded and clean pastures, respectively. *Theobroma cacao* L. had 1.11% relative abundance, but is considered as natural regeneration of the individuals planted in the mixed tree plantations (Table 3).

Palmares II

	ExpFor	BurnFor	OldSec	YoungSec	AnnCrop	InvPas	ClePas
Exploited forest	-	118	29	34	44	23	16
Burned forest	0.6	-	39	47	55	34	20
Old secondary forest	0.21	0.34	-	26	22	19	9
Young sec. forest	0.11	0.18	0.2	-	37	23	20
Annual crop	0.12	0.23	0.18	0.53	-	29	23
Invaded pasture	0.09	0.22	0.32	0.32	0.3	-	13
Clean pasture	0.09	0.18	0.14	0.34	0.71	0.37	-

Maçaranduba

	ConFor	ExpFor	OldSec	YoungSec	InvPas	ClePas
Conserved forest	-	86	119	25	20	4
Exploited forest	0.64	-	87	15	13	5
Old secondary forest	0.55	0.54	-	34	27	6
Young sec. forest	0.41	0.4	0.47	-	13	6
Invaded pasture	0.08	0.07	0.19	0.1	-	7
Clean pasture	0.08	0.06	0.08	0.12	0.2	-

Travessão 338S

	ConFor	ExpFor	OldSec	YoungSec	MixTree	InvPas
Conserved forest	-	160	80	43	29	15
Exploited forest	0.72	-	101	66	37	20
Old secondary forest	0.48	0.52	-	40	25	12
Young sec. forest	0.24	0.36	0.33	-	25	10
Mixed tree plantation	0.54	0.46	0.3	0.29	-	11
Invaded pasture	0.12	0.19	0.11	0.18	0.24	-

Similarity level:

- Very high ($h \geq 0.8$)
- High ($0.6 \leq h < 0.8$)
- Medium ($0.4 \leq h < 0.6$)
- Low ($0.2 \leq h < 0.4$)
- Very low ($h < 0.2$)

Figure 2. Horn similarity index of shade-tolerant species (coloured according to the Horn similarity index value range) and number of shared species (in gray) between land use types in the agricultural mosaics of Palmares II, Maçaranduba and Travessão 338S (Pará, Brazil). Land-use acronyms: ConFor = mature conserved forest; ExpFor = mature exploited forest; BurnFor = mature burned forest; OldSec = old secondary forest; YoungSec = young secondary forest; InvPas = invaded pasture; ClePas = clean pasture; AnnCrop = annual crops; MixTree = mixed tree plantation. This figure is in color in the electronic version.

Among all shade-tolerant species (including trees, palms, shrubs and herbs), 10 at Travessão 338S and four at Maçaranduba were present in all or five of the six land-use types within each mosaic, and four species were present in all or six of the seven land-use types present at Palmares II. The species with the highest incidence among land-use types were *Heliconia hirsuta* L.f., present in all land-use types at Palmares II, *Gustavia augusta* L., present in all land-use types at Maçaranduba, and *Astrocaryum gynacanthum* Mart., *Attalea*

maripa (Aubl.) Mart. and *Attalea speciosa*, present in all land-use types at Travessão 338S. *Astrocaryum gynacanthum* also had high incidence at Palmares II and Maçaranduba, and *Gustavia augusta* at Maçaranduba and Travessão 338S (Figure 3).

DISCUSSION

Among the three agricultural mosaics, Maçaranduba and Travessão 338S were the only ones that had conserved mature forest areas without recent signs of human disturbance. The

Table 3. Relative abundance (%) of most abundant shade-tolerant trees and palms in croplands in three agricultural mosaics in the “Arc of Deforestation” region, Pará state, Brazil. Highest scores of relative abundance in each land-use type are in bold. Land-use acronyms: ConFor = mature conserved forest; ExpFor = mature exploited forest; BunFor = mature burned forest; OldSec = old secondary forest; YoungSec = young secondary forest; InvPas = invaded pasture; ClePas = clean pasture; AnnCrop = annual crops; MixTree = mixed tree plantation.

Species	Life form	Palmares II			Maçaranduba		Travessão 338S	
		AnnCrop	InvPas	ClePas	InvPas	ClePas	MixTree	InvPas
<i>Alexa grandiflora</i>	Tree	0.001	0.33	0	0.002	0	0	0
<i>Annona exsucca</i>	Tree	0.06	0.35	0	0	0	0.005	0
<i>Astrocaryum gynacanthum</i>	Palm	0.09	0.003	0	0.12	0	0.14	0.008
<i>Attalea speciosa</i>	Palm	0	0	0	0.005	0	0.49	0.05
<i>Enterolobium shomburgkii</i>	Tree	0	0	0.07	0	0	0	0
<i>Eugenia patrisii</i>	Tree	0	0	0	0.3	0	0	0
<i>Geissospermum vellosii</i>	Tree	0.12	0.33	0.07	0	0	0	0
<i>Gustavia augusta</i>	Tree	0	0	0	0.06	0.06	0.02	0
<i>Handroanthus serratifolius</i>	Tree	0	0	0	0.3	0	0	0
<i>Jacaranda copaia</i>	Tree	0	0	0	0	0.13	0.04	0
<i>Ocotea cernua</i>	Tree	0	0	0	0	0	0.27	0
<i>Pachira aquatica</i>	Tree	0	0	0	0	0.06	0	0
<i>Protium sagotianum</i>	Tree	0	0	0	0	0	0	0.1
<i>Rinorea neglecta</i>	Tree	0	0	0	0	0	0	0.1
<i>Senna georgica</i>	Tree	0.09	0	0	0	0	0	0
<i>Siparuna guianensis</i>	Tree	0	0	0	0.18	0	0	0
<i>Tabernaemontana macrocalyx</i>	Tree	0	0	0.14	0	0	0	0
<i>Theobroma cacao</i>	Tree	0	0	0	0	0	1.11	0
<i>Trichilia sp.</i>	Tree	0	0	0	0	0	0	0.2

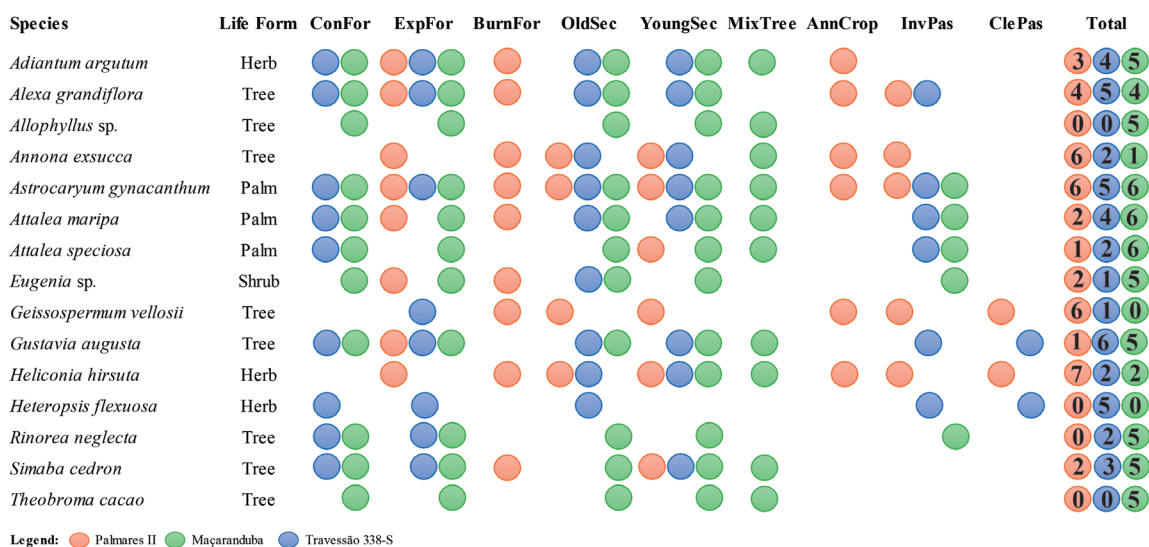


Figure 3. Number of land-use types in which most incident shade-tolerant forest species were present in the agricultural mosaics of Palmares II, Maçaranduba and Travessão 338S (Pará, Brazil). Land-use acronyms: ConFor = mature conserved forest; ExpFor = mature exploited forest; BunFor = mature burned forest; OldSec = old secondary forest; YoungSec = young secondary forest; InvPas = invaded pasture; ClePas = clean pasture; AnnCrop = annual crops; MixTree = mixed tree plantation. This figure is in color in the electronic version.

high similarity of these conserved forests with exploited forests indicates a high maintenance capacity of shade-tolerant species in the forest fragments of the agricultural mosaics, even after selective cutting. Indeed, selective logging has been considered a disturbance that can maintain high rates of forest richness, even though there is a biodiversity-reducing effect, but much lower when compared to other types of human disturbance (Gibson *et al.* 2011).

The same level of conservation could not be confirmed at Palmares II, as all of its forest fragments were disturbed. Additionally, exploited forests at Palmares II were highly similar with burned forests, which were expected to present the highest reduction in biodiversity, since plants are the biological group most sensitive to fire (Gibson *et al.* 2011) (although fire intensity and frequency influences the extent of the disturbance). This result may imply a higher level of impact of logging on biodiversity in already fragmented and disturbed landscapes. Disturbances within the forest fragments, when combined with disturbances of a highly degraded landscape, result in greater negative effects on biodiversity, especially on species of high conservation value and functionality (Barlow *et al.* 2016). The negative effects on biodiversity conservation at Palmares II were also suggested by the low or very low similarity between the disturbed mature forests and secondary forests, which indicates a delay in the progression of forest succession, probably caused by a functionally reduced species-rich forest cover in the landscape (Van Breugel *et al.* 2013; Do Vale *et al.* 2018).

Conservation of mature forests and species-rich secondary forests is crucial for biodiversity in tropical human-disturbed landscapes (Vieira and Proctor 2007; Rozendaal *et al.* 2019), since it can accelerate forest succession by providing non-degraded soils, abundant sources of propagules for plant regeneration, seeds, soil seed bank, seedling bank and sprouts, as well as reduced filtering imposed by site conditions, edge effects and resource exploitation by human populations (Arroyo-Rodríguez *et al.* 2017). At Maçaranduba and Travessão 338S, medium similarity between mature forests and old secondary forests points to a greater landscape connectivity in these mosaics, and, therefore, greater conservation potential. It also demonstrates that old secondary forests can maintain high richness and abundance of shade-tolerant species, playing an important role for conservation, particularly when landscapes present higher forest cover, low intensity of previous land use and presence of more conserved forests.

Presence of shade-tolerant forest species in agricultural land-use types was lower in both active and abandoned crops. At Palmares II, high similarity between annual crops and clean pastures revealed a favorable habitat for a group of shade-tolerant forest species that can persist in both environments. However, environmental heterogeneity established between invaded and clean pastures favored different arrays of forest

species. The difference between types of pastures is probably due to time since abandonment of the invaded pastures, where previous woody species colonization can cause additional positive effects on future natural regeneration (Rocha *et al.* 2016). Despite this invasion, adjacent forest cover seems to have limited influence on these land use types, as shown by the overall low similarity between invaded pastures and the forest land-use types. This is probably due to the limited range of animal dispersers in open environments, and also because invaded pastures – in spite of their woody component - have very different environmental conditions than surrounding forests, restricting the establishment of many shade-tolerant species even among those that are able to arrive (Letcher and Chazdon 2009; Rocha *et al.* 2016).

In contrast, mixed tree plantations showed medium similarity with old secondary forests at Travessão 338S, which was expected, since annual crops and pastures have greater negative impact on biodiversity than agroforestry systems and shaded plantations (Gibson *et al.* 2011). Mixed plantations of native trees generally promote more adequate environmental conditions for shade-tolerant forest species, such as the establishment of a more favorable microclimate, higher concentration of organic matter, lesser soil erosion and higher attraction of dispersing agents (Akoto *et al.* 2015; Zermeño-Hernández *et al.* 2015).

Although agricultural mosaics can provide important habitat and foraging sites for forest species, as well as stepping stones and corridors for biotic dispersal and animal migration, managed croplands have typically a lower biodiversity value than more complex environments, such as secondary forests and mixed plantations (Laurance *et al.* 2014; Do Vale *et al.* 2017). However, shade-tolerant forest species that can maintain a minimum density in croplands can be used for forest restoration, as they improve seed dispersal, attracting animal dispersers and improving seed rain and the seed bank, and provide a more favorable microclimate for the establishment of seedlings and shade herbaceous species (Holl *et al.* 2000; Stanturf *et al.* 2014).

Among trees that were present in the studied croplands, we can highlight *Alexa grandiflora* Ducke, *Annona exsucca*, *Geissospermum vellosii*, *Gustavia augusta* and *Rinorea neglecta* Sandwith, which were the most representative in density and incidence in one or more croplands at the agricultural mosaics. However, insufficient knowledge of the collection, storage, germination and nursery cultivation requirements of these species may presently limit their potential use in forest restoration management programs (Hooper *et al.* 2005).

The importance of palm trees in croplands must also be underlined. *Astrocaryum gynacanthum*, *Attalea maripa* and *Attalea speciosa* were some of the most dense and incident species at the mosaics. They have a great capacity for colonization and are commonly found in other open areas of

southeastern Pará State, where this study was conducted (Salm *et al.* 2005; Santos and Mitja 2011). They have large seeds and are moderately to highly shade-tolerant, attributes that are recommended for species to be used in forest restoration (Hooper *et al.* 2002). Moreover, these palm trees are resistant to the slash-and-burn cultivation system used in family farming (Mitja *et al.* 2008, 2017; Santos and Mitja 2011). Fire can stimulate the germination of seeds that were buried in the soil by grazing (Shanley and Medina 2005). These palms can grow and reproduce faster after disturbing events, because their columnar architecture provides advantages in competition with ephemeral pioneers such as lianas, which can facilitate the restoration in height and density of the secondary forest canopy (Salm *et al.* 2005).

CONCLUSIONS

Agricultural mosaics can maintain high conservation potential of shade-tolerant species in forest fragments that have undergone different levels of disturbance. This potential is higher in mature forests, even if they were exploited. However, the conservation potential of shade-tolerant species was lower in secondary forests found at the most fragmented and human-disturbed mosaic. This suggests that the conservation of mature forests and the maintenance of landscape connectivity is crucial to the maintenance of shade-tolerant species in forest fragments across the landscape. Shade-tolerant forest species showed very low densities in croplands, but a similar assemblage seemed to colonize annual crops and clean pastures, while in invaded pastures other species were present. To consider the difference between croplands is a step further to improve species selection for forest restoration. There is also a need for research in cultivation and implementation requirements of these species, since most have little or no information related to its silviculture.

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