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Tree Regeneration Under Different Land-Use Mosaics in the Brazilian Amazon's "Arc of Deforestation"

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Abstract We studied the tree-regeneration patterns in three distinct agricultural settlements in the Eastern Amazon to test the influence of land-use mosaics. The following questions are addressed: are the floristic structure and composition of regenerating trees affected by the various land-use types applied in the agricultural settlements? Do tree-regeneration patterns respond similarly to distinct land-use mosaics? Is there a relationship between tree regeneration and soil characteristics among the land-use types? The regeneration was inventoried at 45 sampling points in each settlement. At each sampling point, fourteen soil variables were analyzed. Nine different land-use types were considered. The floristic structure and composition of the settlements showed differences in the density of individuals and species and high species heterogeneity among the land-use types. The maximum Jaccard similarity coefficient found between land-use types was only 29 %. Shade-tolerant species were the most diverse functional group in most land-use types, including pasture and annual crops, ranging from 91 % of the number of species in the conserved and exploited forests of Travessão 338-S to 53 % in the invaded pastures of Maçaranduba. The land-use types influenced significantly the floristic structure and composition of regenerating trees in two agricultural settlements, but not in third the settlement, which had greater forest cover. This finding demonstrates that the composition of each land-use mosaic, established by different management approaches, affects regeneration patterns. Tree regeneration was related to soil characteristics in all mosaics. Preparation of the area by burning was most likely the determining factor in the differences in soil characteristics between forests and agricultural areas.

Keywords Biodiversity · Land-use types · Conservation · Family farm · Landscape

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Introduction

In the Amazon, frequent changes in land use have created mosaics consisting of disturbed fragments with various uses interconnected by natural areas in a single landscape (Costa et al. 2012). The habitat heterogeneity found in such landscapes meets a range of biological and ecological functions (such as refuge, nutrition, and dispersal corridors) that aid species diversity and survival (Benton et al. 2003). There is increasing evidence that the distribution and abundance of populations and their biotic interactions often rely on processes occurring at larger spatial scales than the local habitat, i.e., landscape scale, as in land-use mosaics (Grimaldi et al. 2014; Tscharntke et al.2005; Vandermeer and Carvajal 2001). However, further studies on the biodiversity-conservation capacity of such agroecosystems are needed (Asner et al. 2009; Perfecto and Vandermeer 2008; Vandermeer and Perfecto 2007).

To assess the biological-conservation potential of these landscapes, it is important to understand species-regeneration patterns because these patterns are defined by the disturbance regime (including the intensity, frequency, and scale of disturbance) and species biology (including life history, physiology, and behavior) (Kennard et al. 2002). The disturbances are related to the various land-use types and their histories; species biology is related to the biotic and abiotic environmental context (Benjamin et al. 2005; Flinn and Vellend 2005).

Disturbances caused by crop establishment can follow various trajectories involving the intensification of soil use, crop rotation, degradation, and inactivity of the area (Alves 2007; Alves et al. 2009; Mesquita et al. 2001). These usage patterns can affect environmental factors, such as soils, which influence the productivity and structure of the land-use types in various ways (Grimaldi et al. 2014). Forest fragments embedded in agricultural landscapes can strongly influence crops by serving as a source of propagules for the establishment of species that colonize cultivated areas (Jules and Shahani 2003).

Thus, species-regeneration patterns may result in part from the initial setting (the initial environment and remnant forest fragments) in addition to the land use itself (D'Orangeville et al. 2008; Flinn and Vellend 2005). These patterns are affected by the selection of available micro-habitats after disturbances and/or by resource limitations due to competition among individuals (Benton et al. 2003; Liira et al. 2011; Prevedello and Vieira 2010). Thus, various fragmented landscapes with similar forests, soils, climates, ages, and land-use histories can diverge dramatically in terms of species composition and dynamics (Laurance et al. 2011).

Trees are an excellent functional group for analyzing biodiversity conservation in the Amazon due to its large number of species in the region: approximately 16,000 species with a diameter at breast height (DBH) >10 cm (ter Steege et al. 2013). The relative abundance of tree species reflects the progression of forest succession. Trees are important to the regional economy; timber is the most marketable extractive commodity in old-growth tropical forests and accounts for >90 % of the revenues from forests of the nine Brazilian Amazonian states (IBGE 2006).

In this context, the aim of the present study is to describe, analyze, and compare the tree-regeneration patterns in three distinct agricultural settlements in the Eastern Amazon to test the influence of land-use mosaics on regeneration. The following questions are addressed: (1) are the floristic structure and composition of regenerating trees affected by the various land-use types applied in the agricultural settlements? (2) Do tree-regeneration patterns respond similarly to distinct land-use mosaics? (3) Is there a relationship between tree regeneration and soil characteristics among the land-use types?

Materials and Methods

Study Area

The study was conducted in three areas with small family farms in the settlements of Maçaranduba, Travessão 338-S, and Palmares II, located in southern and southeastern Pará state, Eastern Amazon, in the region known as the Arc of Deforestation.

The community of Maçaranduba is located in the municipality of Nova Ipixuna in the Praia Alta-Piranheiras Agricultural-Extractivist Settlement Project. This community was established in 1994 and each farm covers 71 ha on average. The community of Travessão 338-S is located along the Trans-Amazonian Highway in the municipality of Pacajá. It was established in 2001 with farms covering 26 ha on average. The Palmares II Settlement Project, located in the municipality of Parauapebas, was established in 1996 with farms covering 86 ha on average. The dominant primary vegetation is tropical rain forest, and the average annual temperature in the study area is approximately 26 °C.

In total, 27 farms were studied, nine in each settlement. All are part of a recent change in landscape dynamics, featuring mosaics that recently were or still are mostly forest. However, the three areas experienced different dynamics. An analysis of the structures of the landscapes in 2007 and its dynamics between 1990 and 2007 was presented by Oszwald et al. (2011). Maçaranduba presents a primarily agricultural landscape, formed about 20 years ago, with many patches of pastures and young secondary forest (10 years old). The remaining forests are relics in riparian zones or in areas of difficult access. The landscape is characterized by a very fast and intense transition from forest to mainly pastures, so the landscape is less complex in terms of fragmentation and diversity. The area of Palmares II presents an agricultural landscape with a younger dynamic than Maçaranduba and older than Travessão 338-S. The landscape is very fragmented, with substantial richness of types of coverage with extensive edges influencing the landscape. This area presents many pastures and secondary herbaceous vegetation, in addition to the presence of recent ground fires in remaining forest areas. The whole area is well served by roads, but the distance between the residential area (Village of Palmares II) and the crops location is the main factor explaining the degree of human impact. The area of Travessão 338-S in Pacajá municipality is the most recently affected by deforestation. It presents a mostly forested landscape, with conversion from forests to agricultural land still at early stages in 2007. The farms properties were primarily forested (90 % of the area) or composed of large forest patches.

Field and Laboratory Methods

Nine small family farms were selected in each of the three settlements. Five sampling points were spaced equally along a transect corresponding either to the longest diagonal of the farm or a roughly north–south axis. The distance between points was thus equal to 1/6 of the transect length and varied according to farm area (200–400 m on average in different farms). Thus, 45 sampling points were surveyed in each settlement for a total of 135 sampling points. The vegetation was inventoried at each sampling point. Because the sampling points were systematically spaced along the diagonal of each farm, they were not selected based on land-use type. Therefore, it was assumed that the plant coverage of the sampling points reflected the mosaic of different land-use types in each settlement, and it was considered as a land-use mosaic.

Nine different land-use types were identified. At Maçaranduba, pastures, secondary, and primary forests made up 44, 30, and 24 % of the sampling points, respectively. At Travessão 338-S, primary forests made up 51 % of the points. At Palmares II, forests, pastures, secondary forests, and annual crops made up 33, 24, 20, and 22 % of the points, respectively (Table 1).

At each sampling point, ten plots of 1 × 1 m were regularly spaced 5 m from each other in a straight line, covering a total of 0.045 ha per settlement and a total sampling area of 0.135 ha. Saplings with heights between 10 and 200 cm (indicating regeneration) were surveyed in each plot. The sum of the density of individuals and number of species found in ten plots per sampling point was used in the analysis, thus only the sampling points were considered as replication. Although trees, shrubs, and palms were collected, for simplicity we refer to them all as trees. The species were classified as pioneer or shade tolerant. Pioneer species occur in open environments and forest gaps; they generally produce many seeds that are viable for long periods on the forest floor. This group also includes secondary species, which are absent from the forest but can rapidly establish themselves in deforested areas. Shade-tolerant species are those whose seeds can germinate under forest shade. The seedlings can establish in forest shade and survive there. Young plants are thus commonly found not only below a canopy, but may also be seen in open environments (Swaine and Whitmore 1988).

Two soil samples were collected from a depth of 0–10 cm to generate a composite sample at each of the 135 sampling points. The following fourteen variables were analyzed: total sand, clay, and silt contents (EMBRAPA 1979); pH_{KCl} (in 1 M KCl:soil solution = 1:2.5); exchangeable H^+ and Al^{3+}, extracted with 0.5 M $(CH3COO)_2Ca$; basic cations (Ca^{2+}, Mg^{2+}, K^+, Na^+), extracted with 1 M KCl; available P, extracted by the Mehlich "double acid" method; and NH^{4+} (Pansu and Gautheyrou 2006). Total carbon and nitrogen were measured by dry combustion using a CHNS elemental analyzer (LECO).

Statistical Analyses

To assess the influence of the land-use types on the structure of tree regeneration, analysis of variance (ANOVA) was used to compare the mean density of individuals and number of species per sampling point between the land-use types of each settlement. Land-use types with less than three sampling points were not considered. ANOVA was also performed to compare the density of individuals and number of species between settlements (Maçaranduba, Travessão 338-S e Palmares II). ANOVA type III was used for uneven sample sizes and Tukey's post hoc test was used for paired comparisons (Systat Software version 12.0). To assess the influence of the land-use types on the floristic composition of tree regeneration, the percentage of shade-tolerant and pioneer species was calculated in each land-use type; this percentage was also used to determine the conservation of shade-tolerant species in each environment. Moreover, the Jaccard coefficient was used to analyze the floristic similarity between the land-use types of each settlement (Brower et al. 1998).

Three principal-component's analyses (PCA), one for each settlement, were applied to test the effect of land-use mosaic on tree generation. Each PCA used a density matrix for the n tree species found in the 45 sampling points from each settlement (205 species at Maçaranduba, 326 at Travessão 338-S, and 238 at Palmares II). These and three additional PCAs were also applied to test the relationship between soil characteristics and tree regeneration in the land-use mosaics. The relationship was tested using a co-inertia analysis between the PCAs for the density matrices of regenerating tree species and the PCAs for the matrices of 14 soil variables from the 45 sampling points in each settlement. Co-inertia analysis compares the structures revealed by PCA analyses, showing whether the co-structure described by the principal axes is similar to the structures seen in the separate analyses of each data matrix (Dolédec and Chessel 1994).

A Monte-Carlo procedure using 999 permutations was applied to test the significance of the relationship between the floristic groups and soil characteristics within the land-use types showed in the PCAs and to test the significance of the co-inertia analysis. The software ADE-4 (Thioulouse et al. 1997), included in R version 3.0.1 (R Development Core Team 2013), was used. The significance level for all tests was set at 5 % probability. For the multivariate analyses (PCA and co-inertia), the matrices of the species

Table 1 Number of sampling points per land-use type at three agricultural settlements (Maçaranduba, Travessão 338-S, and Palmares II) in the arc of deforestation region, Pará State, Brazil

Land-use type	Description	Maçaranduba	Travessão 338-S	Palmares II	Total
Conserved forests	Forests with a well-defined vertical structure and no signs of human disturbance	8	7	–	15
Exploited forests	Forests showing signs of disturbance, such as clearings resulting from timber extraction	3	16	5	24
Burned forests	Forests showing signs of fire	–	–	10	10
Old secondary forest	Secondary forests with a defined woody upper canopy, older than 12 years	9	4	3	16
Young secondary forest	Secondary forests lacking a defined upper woody stratum, younger than 12 years old	4	5	6	15
Invaded pastures[a]	Pastures with a high abundance of herbaceous individuals and young seedlings of woody species	11	6	4	21
Clean pastures[a]	Pastures with a low density of woody species	9	1	7	17
Annual crops	Rice (*Oryza* sp.), bean (*Vigna* sp.), corn (*Zea mays*) and especially cassava (*Manihot esculenta*) plantations	1	2	10	13
Perennial crops (cocoa)[b]	Cocoa (*Theobroma cacao*) plantations, generally combined with paricá (*Schizolobium amazonicum*)	–	4	–	4
Total	Total sampling points	45	45	45	135

[a] *Brachiaria brizantha* was the predominant forage at Maçaranduba and Palmares II, while *Brachiaria decumbens* predominated at Travessão 338-S

[b] Perennial crops are uncommon in southeastern Pará and were restricted to Travessão 338-S, which is part of the cocoa-producing region in southern Pará

density and soil variables were log-transformed [$\text{Log}_{10}(x + 1)$] to decrease the weight of the abundant species and increase the weight of the rare species and to gauge the distinct soil variables.

Results

Sapling Density and Number of Species

In total, 1506, 1747, and 1420 saplings representing 205, 326, and 238 species were recorded at Maçaranduba, Travessão 338-S, and Palmares II, respectively. The density of individuals at each sampling point showed large variation, with a minimum of zero in annual crops and 137 individuals in exploited forest. The density of individuals and numbers of species in secondary forests were intermediate between those in forests and agricultural areas. Travessão 338-S had the highest mean number of species in total (18 ± 1; mean ± standard error) between Palmares II (12 ± 1) and Maçaranduba (10 ± 1) (ANOVA; $F_{2,132} = 6.735$; $P = 0.002$), but the density of individuals did not differ significantly between settlements (ANOVA; $F_{2,132} = 0.698$; $P = 0.499$). Maçaranduba, Travessão 338-S, and Palmares showed total mean density of 33 ± 5, 39 ± 4, and 32 ± 4, respectively (Fig. 1).

At Maçaranduba alone, saplings were most abundant in conserved (76 ± 10), exploited (68 ± 4), and old secondary forests (48 ± 12) and less abundant in invaded (11 ± 3) and clean pastures (3 ± 1) (ANOVA; $F_{5,38} = 13.77$; $P = 0.000$). The mean number of species showed similar pattern (ANOVA; $F_{5,38} = 20.41$; $P = 0.000$). At Travessão 338-S, fewer saplings were found in invaded pastures (5 ± 2) than in conserved (45 ± 4), exploited (51 ± 5), and in old secondary forests (50 ± 25) (ANOVA; $F_{5,36} = 4.46$; $P = 0.003$). Furthermore, fewer species occurred in invaded pastures (3 ± 1), young secondary forests (13 ± 3), and cocoa plantations (13 ± 1) than in conserved (26 ± 2) and exploited forests (25 ± 2) (ANOVA; $F_{5,36} = 13.43$; $P = 0.000$). At Palmares II, the largest numbers of saplings occurred in exploited (65 ± 21) and burned forests (50 ± 10), similarly with old (45 ± 12) and young (22 ± 5) secondary forests and invaded pastures (37 ± 7), while fewer saplings occurred in clean pastures (4 ± 2) and annual crops (15 ± 4) (ANOVA; $F_{6,38} = 5.49$; $P = 0.000$). Clean pastures (2 ± 1), annual crops (7 ± 1), and young secondary forests (8 ± 1) had fewer regeneration tree species than conserved (24 ± 5) and burned forests (21 ± 3). However, invaded pastures had similar species numbers to burned forests but fewer species than exploited forests with mean species of 10 ± 2 (ANOVA; $F_{6,38} = 20.41$; $P = 0.000$) (Figs. 2, 3).

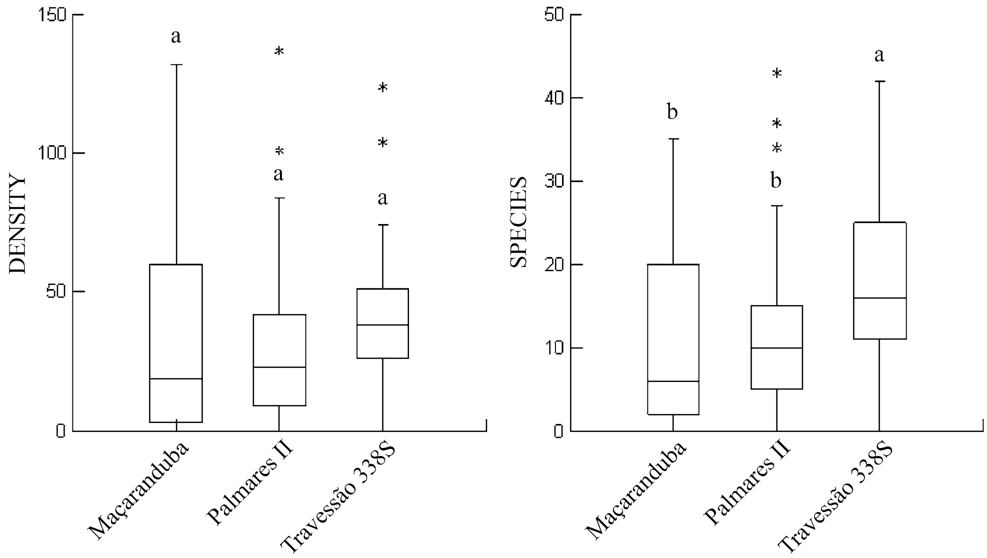

Fig. 1 *Box plot* of the density and number of species of tree regeneration per sampling point of three agricultural settlements in southeastern Pará. *Different letters* indicate significant differences between the settlements (ANOVA type III, $P < 0.05$)

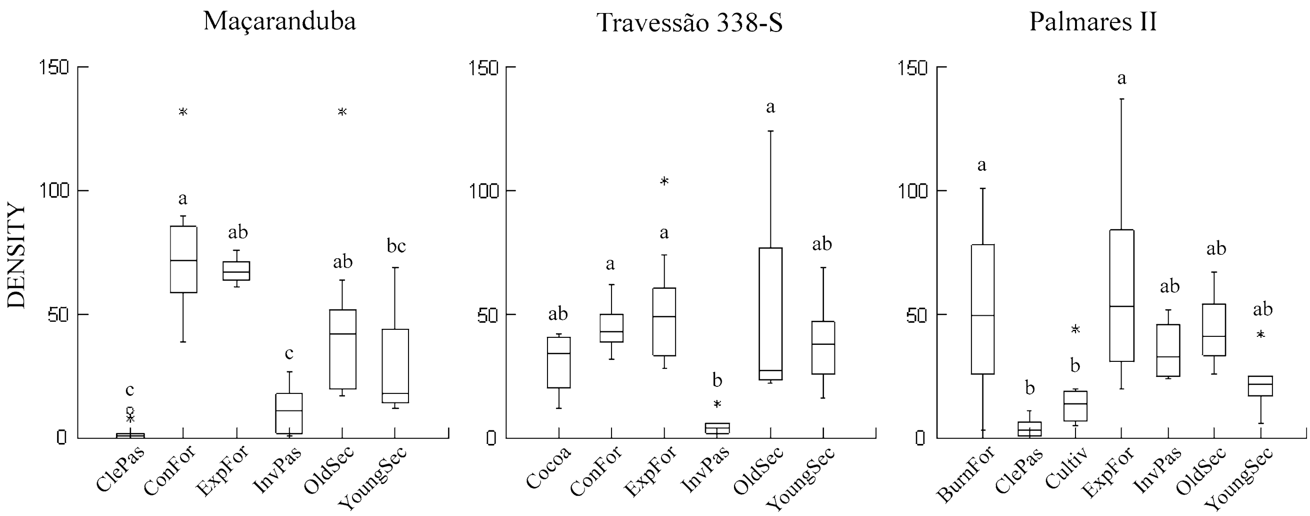

Fig. 2 *Box plot* of the density for tree regeneration per sampling point by land-use type at three agricultural settlements in southeastern Pará. *Different letters* indicate significant differences between land-use types within each settlement (ANOVA type III, $P < 0.05$). *ConFor* conserved forest, *ExpFor* exploited forest, *BurFor* burned forest, *OldSec* old secondary forest, *YoungSec* young secondary forest, *InvPas* invaded pasture, *ClePas* clean pasture, *Cultiv* annual crops, *Cocoa* cocoa plantation

At all three settlements, the diversity of shade-tolerant species was greater than pioneer species in all land-use types, except in clean pastures at Palmares II and Travessão 338-S. However, the number of samples of clean pastures at Travessão 338-S (one sampling point) was not representative. The percentage of shade-tolerant species ranged from 91 % in the conserved and exploited forests of Travessão 338-S to 53 % in the invaded pastures of Maçaranduba. Considering only pioneer species, the diversity was greater in agricultural areas (ranging from 47 % in invaded pastures of Maçaranduba to 33 % in clean pastures of Maçaranduba and annual crops of Palmares II) than in forests (ranging from 13 % in exploited forests of Maçaranduba to 9 % in conserved and exploited forests of Travessão 338-S) (Fig. 4).

The differences between land-use types increased when considering the percentage of individuals of pioneer species, which were the majority in agricultural areas ranging from 76 % in clean pastures of Palmares II to 52 % in clean pastures of Maçaranduba. Shade-tolerant species were more numerous in other land-use types, ranging from 97 % of individuals in the old secondary forests of Travessão 338-S to 61 % in burned forests of Palmares II. Young secondary forests at Maçaranduba were the

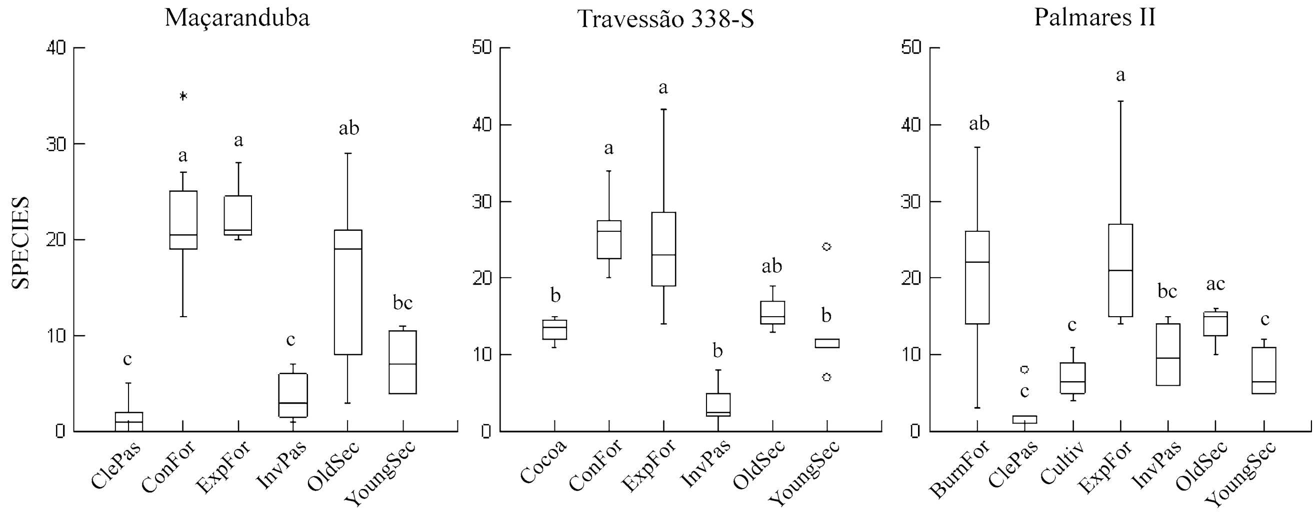

Fig. 3 *Box plots* of the numbers of species for tree regeneration per sampling point by land-use type at three agricultural settlements in southeastern Pará. *Different letters* indicate significant differences between land-use types within each settlement (ANOVA type III, $P < 0.05$). *ConFor* conserved forest, *ExpFor* exploited forest, *BurFor* burned forest, *OldSec* old secondary forest, *YoungSec* young secondary forest, *InvPas* invaded pasture, *ClePas* clean pasture, *Cultiv* annual crops, *Cocoa* cocoa plantation

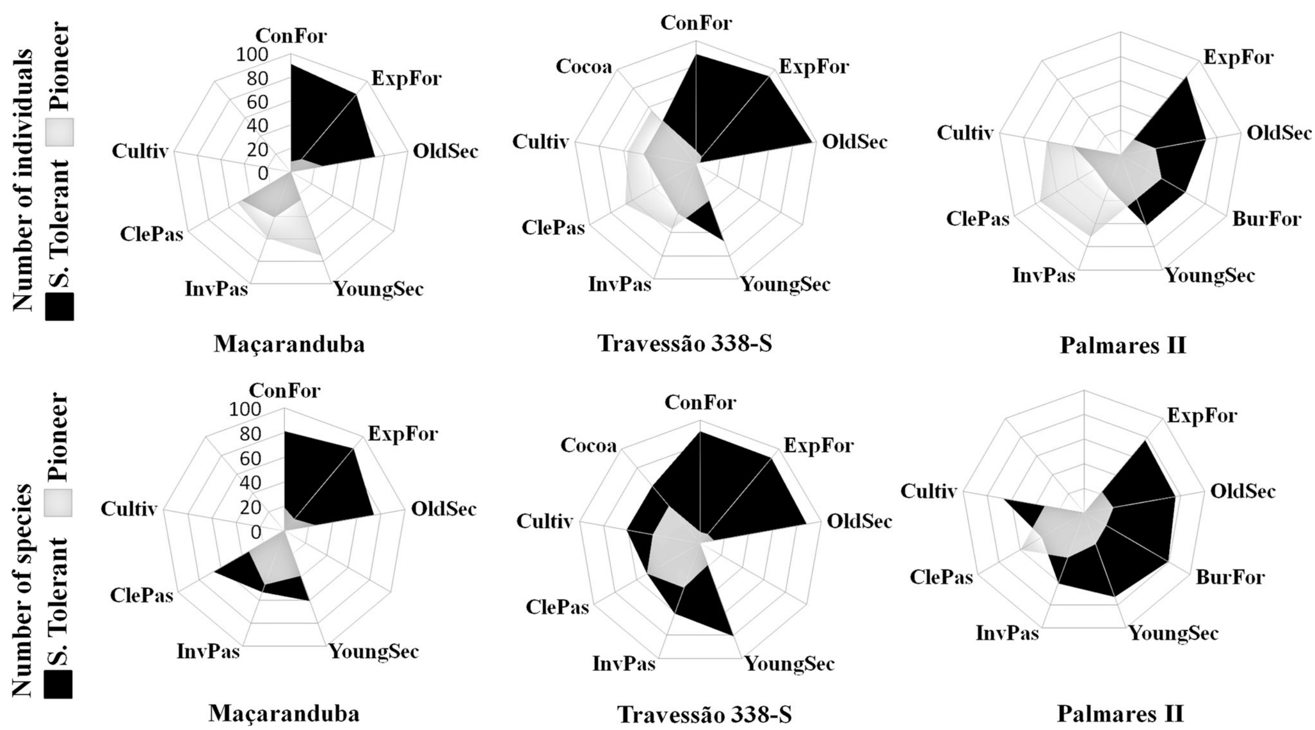

Fig. 4 Percentages of individuals and species belonging to two ecological groups [pioneer species (*gray*) are superimposed on shade-tolerant species (*black*)] in each land-use type at Maçaranduba, Travessão 338-S, and Palmares II. *ConFor* conserved forest, *ExpFor* exploited forest, *BurFor* burned forest, *OldSec* old secondary forest, *YoungSec* young secondary forest, *InvPas* invaded pasture, *ClePas* clean pasture, *Cultiv* annual crops, *Cocoa* cocoa plantation

exception, where pioneer species dominated with 75 % of individuals (Fig. 4). The burned forest at Palmares II presented the largest number of pioneer saplings among forests samples (39 %).

The species composition was highly heterogeneous among the land-use types in each studied area. The maximum Jaccard similarity coefficient, found between conserved and exploited forests at Travessão 338-S, was only 29 %.

Influence of Land-Use Mosaics on Tree Regeneration

The land-use types explained 23 and 22 % of the variability in regeneration at Maçaranduba and Palmares II, respectively (Monte-Carlo test; $P < 0.01$). In those settlements, the PCA yielded clusters that differentiated the regeneration of the different land-use types along the first two ordination axes (Fig. 5a, c). At Travessão 338-S, the PCA results were not significant (Monte-Carlo test; $P > 0.05$; Fig. 5b).

At Maçaranduba, axis 1 explained 17 % of the variance in the data (eigenvalue = 2.78) and differentiated the forests and old secondary forests—which were both characterized by the shade-tolerant species *Astrocaryum gynacanthum*, *Bauhinia guianensis*, and *Inga edulis* – from the pastures, which were influenced by the pioneer species *Banara guianensis*, *Piper graciliramosum*, and *Vismia guianensis*. The sampling points of conserved forest, exploited forest, old secondary forest, invaded pasture, and clean pasture accounted for 38, 14, 24, 10, and 8 % of the first axis, respectively. Axis 2 explained 8 % of the variance (eigenvalue = 1.33) and differentiated the conserved forest—characterized by *Inga paraensis* and *Inga auristellae*—from the exploited forest and old secondary forest, which were strongly influenced by *Inga edulis* (Fig. 5a). The conserved forest, exploited forest, and old secondary forest sampling points accounted for 76, 12, and 10 % of the second axis, respectively.

At Palmares II, axis 1 explained 14 % of the variance in the data (eigenvalue = 2.06) and differentiated the exploited forest, which was strongly influenced by the shade-tolerant species *Amphiodon effusus*, *Protium apiculatum*, and *Psychotria deflexa*, from the burned forest, which was influenced by the pioneer species *Cecropia obtusa* and *Solanum rugosum*. The exploited forest and burned-forest sampling points accounted for 50 and 33 % of the first axis, respectively. Axis 2 explained 10 % of the variance (eigenvalue = 1.58) and differentiated the forest land-use types, which were influenced by the pioneer species *Aparisthmium cordatum*, *Cecropia palmata*, and *Solanum rugosum*, from the invaded pastures and annual crops, which were mostly influenced by the pioneer species *Solanum acanthodes* and *Trema micrantha* (Fig. 5c). The exploited forest, burned forest, invaded pasture, and annual crops sampling points accounted for 15, 54, 15, and 10 % of the second axis, respectively.

Relationships Between Soil Characteristics, Land-Use Types, and Tree Regeneration

According to the PCA of the 14 soil variables, the land-use types explained 24 and 29 % of the variability in soil characteristics at Maçaranduba and Palmares II, respectively (Monte-Carlo test; $P < 0.01$; Fig. 6a, c). However, as in the species-abundance analysis, the PCA was not significant for Travessão 338-S (Monte-Carlo test; $P > 0.05$; Fig. 6b).

At Maçaranduba, axes 1 and 2 explained 36 and 25 % of the variance in the data, respectively, with eigenvalues of 5 and 3.51. These axes differentiated the forests and old secondary forest—which were both characterized by higher levels of total clay, silt, carbon, nitrogen, and exchangeable acids (Al^{3+} and H^+)—from young secondary forests and pastures, which had higher levels of sand and exchangeable bases (Ca^{2+}, Mg^{2+}, and K^+) and a higher pH_{KCl}. Similar

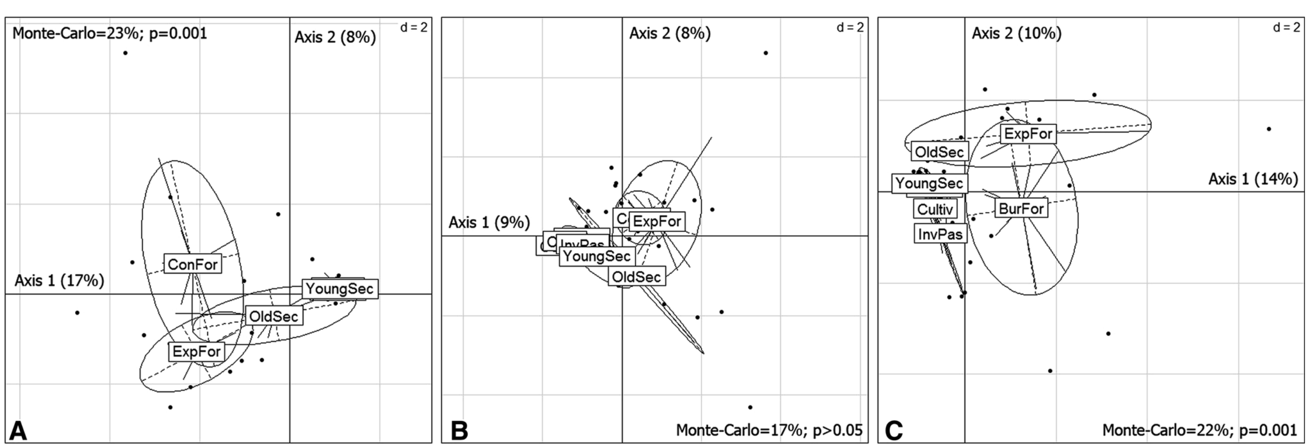

Fig. 5 Principal-component analysis of species log (abundance +1) at 45 sampling points in each settlement **a** Maçaranduba (205 regenerating tree species), **b** Travessão 338-S (326 species), **c** Palmares II (238 species). Projection of clustered points by land-use type (*ConFor* conserved forest, *ExpFor* exploited forest, *BurFor* burned forest, *OldSec* old secondary forest, *YoungSec* young secondary forest, *InvPas* invaded pasture, *ClePas* clean pasture, *Cultiv* annual crops, *Cocoa* cocoa plantation). *Circles* represent the mean (centroid) of the coordinates for each land-use type in factorial space. *Values* in *parentheses* represent the projected inertia for each axis

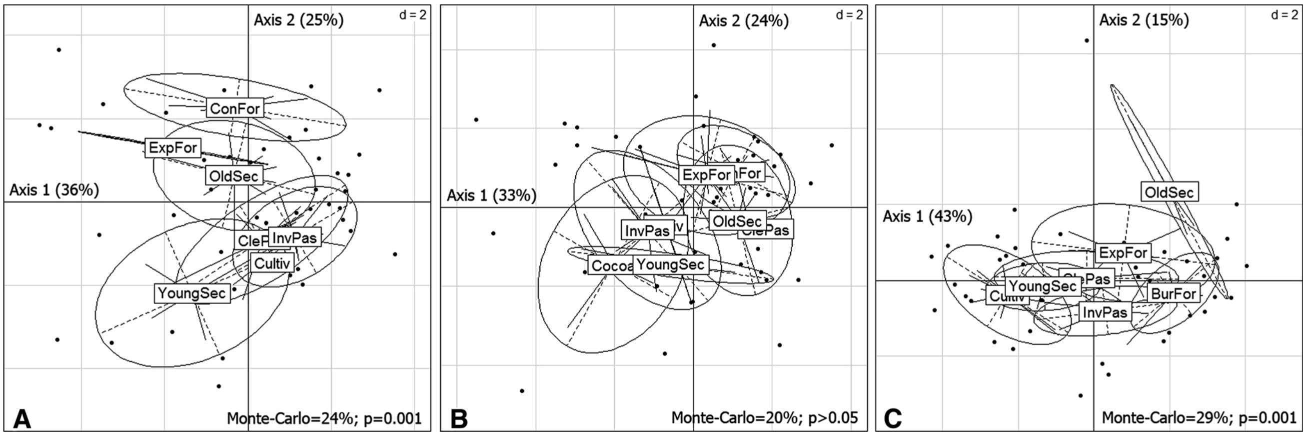

Fig. 6 Principal-component analysis of 14 soil variables at 45 sampling points in each settlement: **a** Maçaranduba, **b** Travessão 338-S, **c** Palmares II. Projection of clustered points by land-use type (*ConFor* conserved forest, *ExpFor* exploited forest, *BurFor* burned forest, *OldSec* old secondary forest, *YoungSec* young secondary forest, *InvPas* invaded pasture, *ClePas* clean pasture, *Cultiv* annual crops, *Cocoa* cocoa plantation). *Circles* represent the mean (centroid) of the coordinates for each land-use type in factorial space. *Values* in *parentheses* represent the projected inertia for each axis

Fig. 7 Co-inertia analysis between the principal-component analysis of species abundance and soil characteristics at 45 sampling points in each settlement. **a** Maçaranduba, **b** Travessão 338-S, **c** Palmares II. Projection of clustered points by land-use type. *ConFor* conserved forest, *ExpFor* exploited forest, *BurFor* burned forest, *OldSec* old secondary forest, *YoungSec* young secondary forest, *InvPas* invaded pasture, *ClePas* clean pasture, *Cultiv* annual crops, *Cocoa* cocoa plantation

results were obtained at Palmares II. Axes 1 and 2 explained 43 and 15 % of the variance in the data, respectively, with eigenvalues of 6.05 and 2.08. These axes differentiated the forests and old secondary forest, which both had higher levels of total clay, ammonia, carbon, nitrogen, and exchangeable acids (Al^{3+} and H^{+}), from annual crops and clean pastures, which had higher levels of sand and exchangeable bases (Ca^{2+}, Mg^{2+}, and K^{+}) and a higher pH_{KCl}.

The co-inertia analysis showed that the structure of the species-abundance matrix was similar to that of the soil characteristics matrix for all settlements, explaining 31, 32, and 25 % of the variability at Maçaranduba, Travessão 338-S, and Palmares II, respectively (Monte-Carlo test; $P < 0.05$; Fig. 7).

Discussion

Despite the low percentage of explanation (below 20 %) found in the first axis of the PCAs for the floristic data, the land-use types influenced significantly the floristic structure and composition of regenerating trees and the soil characteristics in the settlements of Maçaranduba and Palmares II; however, this influence was not observed at Travessão 338-S. This finding demonstrates that the influence of land-use types on tree regeneration is manifested at the mesoscale, where the composition of each land-use mosaic, established by different management approaches, affects regeneration patterns.

The results obtained at Travessão 338-S, where the floristic structure and composition and the soil characteristics did not respond to the land-use types, were due to the greater coverage of forests (51 % of the surveyed area) in this settlement. Forests covered only 24 and 33 % of Maçaranduba and Palmares II, respectively. These differences in forest coverage can help in defining the size of forest-protection areas needed to maintain the tree-regeneration potential of the settlements. As we know, the abundance of adjacent forests may increase the probability that forest propagules will be present, thereby strongly influencing the dynamics within settlements (D'Orangeville et al. 2008; Jules and Shahani 2003). Conserved forest fragments embedded in land-use mosaics serve as important sources of dispersal (Vieira and Proctor 2007), pollination, and biological control for agricultural crops (Tscharntke et al. 2005, 2008).

Travessão 338-S also had the most tree species of the surveyed settlements, which can be due to its larger forest area and greater diversity of land-use types with the presence of cocoa plantations, which exhibited regeneration densities similar to those of forests. Thus, the cocoa plantations also contributed to the homogeneous regeneration in the land-use mosaic, relying on the premise that greater habitat diversity permits greater heterogeneity and species variation among individuals (Benton et al. 2003; Schulze et al. 2004). Additionally, tree plantation (unlike herbaceous crops) promote favorable environmental conditions for tree regeneration, such as the establishment of a more favorable microclimate and attraction of dispersal agents (Carnevale and Montagnini 2002; Cusack and Montagnini 2004).

At Maçaranduba and Palmares II, differences between the forest and agricultural environments were reflected by differences among land-use types in number of species and density. The various forest types also exhibited differences, most likely linked to the different disturbances suffered in each area. The disturbance types that occur in forests influence the floristic structure and composition of regeneration (Felton et al. 2006; Holdsworth and Uhl 1997; Kennard et al. 2002). At Maçaranduba, the extraction of timber and non-timber products in the exploited forests probably caused the differences from the conserved forests. At Palmares II, exploited forests differed strongly from burned forests, reflecting the floristic and structural changes that occur after burning.

As expected, the greatest density of individuals and numbers of species of regenerating trees were found in forests. In these areas, the floristic composition was more heterogeneous, with little dominance of one species over another, resulting in a greater quantity of rare species and greater diversity. In agricultural areas, the density of individuals and number of species were lower because most of the individuals and propagules of shade-tolerant species were eliminated during forest removal and because environmental changes indirectly affected tree regeneration (Flinn and Vellend 2005). The dispersal of potential diaspores from forested areas is also restricted by the lack of dispersal agents in open areas (Hooper et al. 2005). As the environment is increasingly modified, the species numbers of various taxonomic groups, such as birds, insects, and mammals, decrease (Barlow et al. 2007; Beck et al. 2002; Schulze et al. 2004). These groups help to disperse and pollinate tropical species. If seeds are present, their survival probability is low due to high competition during cropping periods (Denich et al. 2005). Thus, the low availability of forest propagules combined with environmental conditions of high solar irradiation, high evapotranspiration, altered soils, herbaceous competition, and disturbance during soil preparation and weeding limits tree regeneration in cropped areas (Esquivel et al. 2008; Hooper et al. 2005; Nesptad et al. 1996), reducing density and species numbers.

Differences between young and old secondary forest are associated with the time elapsed since agricultural activity ended, known as the fallow time; biodiversity tends to increase over time (Chadzon et al. 2009; Coelho et al. 2003; Vieira et al. 2003). Old secondary forests were similar in species numbers to forests, while young secondary forests had fewer species in all three settlements. Young secondary forests of Maçaranduba were also dominated by pioneer species, being an exception between forests and secondary forests that were dominated by shade-tolerant species, probably related to its younger age. Despite the differences, secondary forests played an important role in biodiversity conservation and recomposition in all three studied areas, with their density and number of species being intermediate between those of forests and agricultural areas. This transitional behavior between natural and anthropic environments is related to the forest-succession process. The role of secondary forests in species conservation has been stressed in the literature (Barlow et al. 2007; Chadzon et al. 2009; Schulze et al. 2004).

In agricultural areas, during the first stages of floristic succession (Mitja et al. 2008), regeneration mainly occurs from the seed bank and/or seed rain and consists mostly of pioneer species, while shade-tolerant species emerge mainly by sprouting from forest-vegetation remnants (Vieira and Proctor 2007). Therefore, the greater density of pioneer species in agricultural areas was linked to environmental conditions of high solar irradiation. Nevertheless, shade-tolerant species were the most diverse functional group in most land-use types, including agricultural areas, demonstrating the significant capacity of these open environments for shade-tolerant species conservation when inserted in a matrix where forests fragments are present. The distance from the forest is most important when vegetation such as trees and shrubs are not found in early successional stages (Slocum and Horvitz 2000; Hooper et al. 2005). This result also supports the concept of reforestation via installation of pioneer and shade-tolerant species coexisting since the beginning of the succession (Mitja et al. 2008), although with different densities.

The exceptions were the clean pastures at Palmares II and Travessão 338-S, where shade-tolerant species did not predominate. In these pastures, the cultivated species *Brachiaria brizantha* (at Palmares II) and *Brachiaria decumbens* (at Travessão 338-S) may have contributed to the reduction in shade-tolerant species. The development of woody vegetation is inversely related to the presence of herbaceous species, especially in *B. decumbens* pastures. Management practices that include removing or reducing the effects of *Brachiaria* spp. in restoring abandoned pastures may be needed to stimulate natural regeneration (Cheung et al. 2009). Mitja and Miranda (2010) have also confirmed that plant diversity and density are influenced by the planted grass species in pastures, with greater regeneration in areas of *Panicum maximum* and less regeneration in areas of *B. brizantha.*

Even in the burned forests at Palmares II, the species were mostly shade-tolerant; however, these sites showed the greatest percentage of pioneer species (39 %) among forests. Fire reduced the canopy cover, biomass, and number of adult trees. Burning decreases the availability of forest-tree propagules, drastically affecting the regeneration of the forest understory and resulting in rapid post-fire colonization by pioneer species (Cochrane and Schulze 1999). The greater number of pioneer species in adjacent burned forests may have facilitated the colonization of the invaded pastures at Palmares II. These invaded pastures were an exception between other pastures in this study, with statistically similar regeneration compared to forests and secondary forests in this area. Pioneer species can disperse over greater distances, are more abundant in both the seed bank, and seed rain (Cochrane and Schulze 1999; Vieira and Proctor 2007). Other factors, such as the land-use history, initial vegetation, crop species, and soil preparation, may have contributed to the greater abundance of trees in the invaded pastures of Palmares II. Santos and Mitja (2011) have also reported dramatic changes in floristic composition in other Amazonian pasture areas, with a greater density of trees and palms in pastures with higher fire frequencies and 64 % of individuals belonging to a single species, *Attalea speciosa*.

Preparation of the area by burning for agriculture was most likely the determining factor in the differences in soil characteristics among the land-use types, especially at the Maçaranduba and Palmares II settlements, whose soil characteristics showed the strongest influence of the land-use types and indirectly affected regeneration. Forest burning in the slash-and-burn system generates ashes (created from the biomass), which release nutrients and increase the pH in agricultural areas (Andreux and Cerri 1989). The soil K, Ca, and Mg levels also rise after burning (Sanchez et al. 1983). At Maçaranduba and Palmares II, soils under pastures and annual crops also showed higher levels of exchangeable bases (Ca^{2+}, Mg^{2+}, and K^{+}) and higher pH_{KCl} values. In older forests, nutrients such as P, K, Ca, and Mg are rapidly absorbed by the vegetation. Thus, after the initial increase in these nutrients due to slashing and burning, the trees that colonize these areas gradually reduce the nutrient concentrations in the soil over time, while most of the C and N remain in the soil (Feldpausch et al. 2004). The forested areas and old secondary forest at Maçaranduba and Palmares II showed lower concentrations of exchangeable bases and higher C and N concentrations in the soils. Carbon levels may decrease in forest soils used for crops and pastures due to erosion, mechanical removal of the topsoil, and greater oxidation of organic material (Detweiler and Hall 1988).

The percentage of clay was lower in the agricultural areas. In pastures, clay levels tend to decrease due to surface erosion and the transport of clay particles to deeper soil layers through water percolation (Lal 1977), making the upper soil layers more sandy. Higher levels of exchangeable acids were found in the forests and old secondary forests of Maçaranduba and Palmares II due to the greater concentrations of Al^{3+} in these areas. This ion can inhibit Ca and Mg absorption (de Wit et al. 2010), reduce the growth of fine roots, alter photosynthetic activity, and lead to nutritional imbalances in forest species (Wright et al. 1989). Similar results were found in a tropical montane cloud forest, in Mexico (Bautista-Cruz et al. 2012), where high Al^{3+} levels may have played an important role in determining plant composition by excluding species that are sensitive to this cation, thus driving the process of natural selection.

Management Applications

The studied land-use mosaics showed a good capacity for conserving tree biodiversity, reflected mainly by the high species heterogeneity among the land-use types. However, the tree-regeneration patterns were not similar across settlements, demonstrating that tree regeneration responds at the mesoscale to different land-use types implemented within agricultural mosaics.

The Brazilian Forest Code (Law 12651/2012) states that 80 % of the area of rural lands in the Amazon biome should be used sustainably (legal reserve area), conserving native vegetation to ensure the maintenance of local biodiversity. For family farming, this law allows tree crops to be considered in addition to native vegetation when calculating the legal reserve area. If this law was applied at the mesoscale, exactly 80 % of the Travessão 338-S area would be a legal reserve (51 % from forests, 20 % from secondary forests, and 9 % from cocoa plantations). Because the land-use types did not appear to affect tree regeneration at Travessão 338-S, we assume that the plant-coverage composition is relevant to the prescriptions of the law; the conservation of native-forest fragments combined with the presence of secondary forests and tree plantation, such as cocoa plantations, played a critical role in reducing the impacts of land-use types on tree biodiversity.

In addition to its distinctive management, Travessão 338-S featured a shorter time since the establishment of farms in 2001 (vs. 1994 at Maçaranduba and 1996 at Palmares II). This difference contributed to the greater conservation of the forest cover. In the other settlements, only 53 % of the area was covered by forest vegetation (conserved and secondary forests). Therefore, we believe that the Brazilian legislation regarding areas to be set aside as Legal Reserves can ensure the conservation of tree biodiversity in the Amazon by maintaining forest fragments embedded in agricultural contexts if the 80 % of forest coverage is guaranteed. However, it is important to consider the environmental quality of such fragments.

Changes in the floristic structure and composition of burned forests at Palmares II, which featured the greatest quantity of pioneer species among forests, demonstrate that the native-plant coverage is strongly affected by fire. Pastures and annual crops have a lower potential for tree regeneration. Such areas are also affected by fire because family farming in the studied region traditionally uses the slash-and-burn system. Using fire-free techniques to prepare the area can help to maintain the potential for tree regeneration, thus improving the conservation potential at the mesoscale. Finally, it is important to consider which crop species could be used in the settlements. The cocoa plantation combined with *Schizolobium amazonicum* showed tree-regeneration densities similar to those of forests. Thus, the use of tree crops can help to maintain tree biodiversity and favor long-term forest recovery in inactive agricultural areas.

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References

Alves DS (2007) Cenários de cobertura e uso da terra e dimensões humanas no LBA. In: Becker BK, Alves DS, Costa WM (eds) Dimensões Humanas da Biosfera-Atmosfera na Amazônia. EDUSP, São Paulo, pp 39–63

Alves DS, Morton DC, Batistella M, Roberts DA, Souza Júnior C (2009) The changing rates and patterns of deforestation and land use in Brazilian Amazonia. In: Keller M, Bustamante M, Gash J, Dias PS (eds) Amazonia and global change, geophysics monograph series, vol 186. AGU, Washington, pp 11–23

Andreux F, Cerri CC (1989) Current trends in the research on soil changes due to deforestation, burning and cultivation in the Brazilian tropics. Toxicol and Environ Chem 20(21):275–283

Asner GP, Rudel TK, Aide TM, DeFries R (2009) Contemporary assessment of global humid tropical forest change. Conserv Biol 23:138–1395

Barlow J, Gardner TA, Araujo IS, Ávila-Pires TC, Bonaldo AB, Costa JE, Esposito MC, Ferreira LF, Hawes J, Hernandez HIM, Hoogmoed MS, Leite RN, Lo-Man-Hung NF, Malcolm JR, Martins MB, Mestre LAM, Miranda-Santos R, Nunes-Gutjahr AL, Overal WL, Parry L, Peters SL, Ribeiro-Junior MA, Silva MNF, Motta CS, Peres CA (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc Natl Acad Sci 104(47):18555–18560

Bautista-Cruz A, Del Castillo RF, Etchevers-Barra JD, Gutiérrez-Castorena MC, Báez A (2012) Selection and interpretation of soil quality indicators for forest recovery after clearing of a tropical montane cloud forest in Mexico. For Ecol Manag 277:74–80

Beck J, Schulze CH, Linsenmair KE, Fiedler K (2002) From forest to farmland, diversity of geometer moths along two habitat gradients on Borneo. J Trop Ecol 18:33–51

Benjamin K, Domon G, Bouchard A (2005) Vegetation composition and succession of abandoned farmland, effects of ecological, historical and spatial factors. Landscape Ecol 20:627–647

Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity, is habitat heterogeneity the key? Trends Ecol Evol 18(4):182–188

Brower JE, Zar JH, Van Ende CN (1998) Field and laboratory methods for general ecology. WCB/McGraw, New York, p 273

Carnevale N, Montagnini F (2002) Facilitating regeneration of secondary forests with the use of mixed and pure plantations of indigenous tree species. For Ecol Manag 163:217–227

Chazdon RL, Peres CA, Dent D, Sheil D, Lugo AE, Lamb D, Stork NE, Miller SE (2009) The potential for species conservation in tropical secondary forests. Conserv Biol 23(6):1406–1417

Cheung KC, Marques MCM, Liebsch D (2009) Relação entre a presença de vegetação herbácea e a regeneração natural de espécies lenhosas em pastagens abandonadas na Floresta Ombrófila Densa do Sul do Brasil. Acta Bot Bras 23(4):1048–1056

Cochrane MA, Schulze MD (1999) Fire as a recurrent event in tropical forests of the eastern Amazon, effects on forest structure, biomass, and species composition. Biotropica 31:2–16

Coelho RFR, Zarin DJ, Miranda IS, Tucker JM (2003) Análise florística e estrutural de uma floresta em diferentes estágios

sucessionais no município de Castanhal. Pará. Acta Amazon 33(4):563–582
Costa LGS, Miranda IS, Grimaldi M, Silva ML Jr, Mitja D, Lima TTS (2012) Biomass in different types of land use in the Brazil's "arc of deforestation". For Ecol Manag 278:101–109
Cusack D, Montagnini F (2004) The role of native species plantations in recovery of understory woody diversity in degraded pasturelands of Costa Rica. For Ecol Manag 188:1–15
D'Orangeville L, Bouchard A, Cogliastro A (2008) Post-agricultural forests, landscape patterns add to stand-scale factors in causing insufficient hardwood regeneration. For Ecol Manag 255:1637–1646
de Wit HA, Eldhuset TD, Mulder J (2010) Dissolved Al reduces Mg uptake in Norway spruce forest, results from a long-term field manipulation experiment in Norway. For Ecol Manag 259:2072–2082
Denich M, Vlek PLG, Sá TDA, Vielhauer K, Lücke W (2005) A concept for the development of fire-free fallow management in the Eastern Amazon, Brazil. Agric Ecosyst Environ 110:43–58
Detwiler RP, Hall CAS (1988) Tropical forests and the global carbon cycle. Science 239:42–47
Dolédec S, Chessel D (1994) Co-Inertia analysis, an alternative method for studying species-environment relationships. Freshw Biol 31:277–294
EMBRAPA (1979) Manual de Métodos de Análise de Solo. Serviço Nacional de Levantamento e Conservação de Solo, Rio de Janeiro
Esquivel JM, Harvey CA, Finnegan B, Casanoves F, Skarpe C (2008) Effects of pasture management on the natural regeneration of neotropical trees. J Appl Ecol 45:371–380
Feldpausch TR, Rondon MA, Fernandes ECM, Riha SJ, Wandelli E (2004) Carbon and nutrient accumulation in secondary forests regenerating on pastures in central Amazonia. Ecol Appl 14:164–176
Felton A, Felton AM, Wood J, Lindenmayer DB (2006) Vegetation structure, phenology, and regeneration in the natural and anthropogenic tree-fall gaps of a reduced-impact logged subtropical Bolivian forest. For Ecol Manag 235:186–193
Flinn KM, Vellend M (2005) Recovery of forest plant communities in post agricultural landscapes. Front Ecol Environ 3:243–250
Grimaldi M, Oszwald J, Dolédec S, Hurtado MP, Miranda IS, Sartre XA, Assis WS, Castañeda E, Desjardins T, Dubs F, Guevara E, Gond V, Lima TTS, Marichal R, Michelotti F, Mitja D, Noronha NC, Oliveira MND, Ramirez B, Rodriguez G, Sarrazin M, Silva ML Jr, Costa LGS, Souza SL, Veiga IP Jr, Velasquez E, Lavelle P (2014) Ecosystem services of regulation and support in Amazonian pioneer fronts: searching for landscape drivers. Landscape Ecol 29(2):311–328
Holdsworth AR, Uhl C (1997) Fire in Amazonian selectively logged rain forest and the potential for fire reduction. Ecol Appl 7(2):713–725
Hooper E, Legendre P, Condit R (2005) Barriers to forest regeneration of deforested and abandoned land in Panama. J Appl Ecol 42(6):1165–1174
IBGE (2006) Censo Agropecuário 2006. Available from http://www.ibge.gov.br. Accessed Dec 2013
Jules ES, Shahani P (2003) A broader ecological context to habitat fragmentation, Why matrix habitat is more important than we thought. J Veg Sci 14:459–464
Kennard DK, Gould K, Putz FE, Morales F (2002) Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. For Ecol Manag 162:197–208
Lal R (1977) Analysis of factors affecting rainfall erosivity and soil erodibility. In: Greenland DJ, Lal R (eds) Soil conservation and management in the humid tropics. Wiley, New York, pp 49–56
Laurance WF, Camargo JLC, Luizão RCC, Laurance SG, Pimm SL, Bruna EM, Stouffer PC, Bruce WG, Benítez-Malvido J, Vasconcelos HL (2011) The fate of Amazonian forest fragments, A 32-year investigation. Biol Conserv 144:56–67
Liira J, Sepp T, Kohv K (2011) The ecology of tree regeneration in mature and old forests, combined knowledge for sustainable forest management. J For Res 16:184–193
Mesquita RCG, Ickes K, Ganade G, Williamson GB (2001) Alternative successional pathways in the Amazon Basin. J Ecol 89:528–537
Mitja D, Miranda IS (2010) Weed community dynamics in two pastures grown after clearing Brazilian Amazonian rainforest. Weed Res 50:163–173
Mitja D, Miranda IS, Velasquez E, Lavelle P (2008) Plant species richness and floristic composition change along a rice-pasture sequence in subsistence farms of Brazilian Amazon, influence on the fallows biodiversity (Benfica, State of Pará). Agric Ecosyst Environ 124:72–84
Nepstad DC, Uhl C, Pereira CA, Silva JM (1996) A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. Oikos 76:25–39
Oszwald J, Gond V, Dolédec S, Lavelle P (2011) Identification d'indicateurs de changement d'occupation du sol pour le suivi des mosaïques paysagères. Bois et Forêts des Tropiques 307(1):8–21
Pansu M, Gautheyrou J (2006) Handbook of soil analysis, mineralogical, organic and inorganic methods. Springer, New York
Perfecto I, Vandermeer J (2008) Biodiversity conservation in tropical agroecosystems, a new conservation paradigm. Ann NY Acad Sci 1134:173–200
Prevedello JA, Vieira MV (2010) Does the type of matrix matter? A quantitative review of the evidence. Biodivers Conserv 19:1205–1223
R. Development Core Team (2013) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Sanchez PA, Villachica JH, Bandy DE (1983) Soil fertility dynamics after clearing a tropical rainforest in Peru. Soil Sci Soc Am J 47:1171–1178
Santos AM, Mitja D (2011) Pastagens arborizadas no projeto de assentamento Benfica, município de Itupiranga, Pará. Brasil Rev Árvore 35(4):919–930
Schulze CH, Waltert M, Kessler PJA, Pitopang R, Shahabuddin DV, Mühlenberg M, Gradstein SR, Leuschner C, Steffan-Dewenter I, Tscharntke T (2004) Biodiversity indicator groups of tropical land-use systems, comparing plants, birds, and insects. Ecol Appl 14:1321–1333
Slocum MG, Horvitz CC (2000) Seed arrival under different genera of trees in a neotropical pasture. Plant Ecol 149:51–62
Swaine MD, Whitmore TC (1988) On the definition of ecological species groups in tropical rain forests. Plant Ecol 75:81–86
ter Steege H et al (2013) Hyperdominance in the Amazonian tree flora. Science 342(6156):1243092
Thioulouse J, Chessel D, Dodelec S, Olivier JM (1997) ADE-4, a multivariate analysis and graphical display software. Stat Comput 7:75–83
Tscharntke T, Rand TA, Bianchi FJJA (2005) The landscape context of trophic interactions, insects spillover across the non-crop interface. Ann Bot Fenn 42:421–432
Tscharntke T, Sekercioglu CH, Dietsch TV, Sodhi N, Hoehn SP, Tylianakis JM (2008) Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology 89:944–951
Vandermeer JH, Carvajal R (2001) Metapopulation dynamics and the quality of the matrix. Am Nat 158:211–220

Vandermeer J, Perfecto I (2007) The agricultural matrix and a future paradigm for conservation. Conserv Biol 21(1):274–277
Vieira ICG, Proctor J (2007) Mechanisms of plant regeneration during succession after shifting cultivation in eastern Amazonia. Plant Ecol 192:303–315
Vieira ICG, Almeida ASD, Davidson EA, Stone TA, Carvalho CJRD, Guerrero JB (2003) Classifying successional forests using Landsat spectral properties and ecological characteristics in eastern Amazonia. Remote Sens Environ 87:470–481
Wright RJ, Baligar VC, Ahlrichs JL (1989) The influence of extractable and soil solution aluminum on root growth of wheat seedlings. Soil Sci 148:292–302