

Structure and composition of altered riparian forests in an agricultural Amazonian landscape

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Abstract. Deforestation and fragmentation influence the microclimate, vegetation structure, and composition of remaining patches of tropical forest. In the southern Amazon, at the frontier of cropland expansion, forests are converted and fragmented in a pattern that leaves standing riparian forests whose dimensions are mandated by the Brazilian National Forest Code. These altered riparian forests share many characteristics of well-studied upland forest fragments, but differ because they remain connected to larger areas of forest downstream, and because they may experience wetter soil conditions because reduction of forest cover in the surrounding watershed raises groundwater levels and increases stream runoff. We compared forest regeneration, structure, composition, and diversity in four areas of intact riparian forest and four areas each of narrow, medium, and wide altered riparian forests that have been surrounded by agriculture since the early 1980s. We found that seedling abundance was reduced by as much as 64% and sapling abundance was reduced by as much as 67% in altered compared to intact riparian forests. The most pronounced differences between altered and intact forest occurred near forest edges and within the narrowest sections of altered riparian forests. Woody plant species composition differed and diversity was reduced in altered forests compared to intact riparian forests. However, despite being fragmented for several decades, large woody plant biomass and carbon storage, the number of live or dead large woody plants, mortality rates, and the size distribution of woody plants did not differ significantly between altered and intact riparian forests. Thus, even in these relatively narrow forests with high edge:area ratios, we saw no evidence of the increases in mortality and declines in biomass that have been found in other tropical forest fragment studies. However, because of the changes in both species community and reduced regeneration, it is unclear how long this relative lack of change will be sustained. Additionally, Brazil recently passed a law in their National Forest Code allowing narrower riparian buffers than those studied here in restored areas, which could affect their long-term sustainability.

Key words: agriculture; Amazon; Brazil; composition; diversity; forest structure; fragmentation; riparian ecosystems.

INTRODUCTION

Deforestation of tropical forests for agriculture is one of the major forces shaping the Earth's surface (Lambin et al. 2003, Lambin and Meyfroidt 2011). In addition to direct loss of forest cover, land conversion fragments remaining forest by creating isolated forest patches and forest edges throughout landscapes (Fearnside 2005, DeFries et al. 2008, Nepstad et al. 2008, Asner et al. 2010). Uncertainty regarding the ability of forest fragments to persist in the landscape and provide ecosystem services has led to a number of studies on fragmentation and edge effects in the Neotropics, from lowland evergreen forests of Brazil to montane cloud forests of Costa Rica (Kapos 1989, Williams-Linera 1990, Oliveira-Filho et al. 1997, Beni-

tez-Malvido 1998, Laurance et al. 1998, 2002, Gascon et al. 2000, Oosterhoorn and Kappelle 2000, Guariguata et al. 2002, Higuchi et al. 2008).

Compared to intact forests, forest fragments in upland areas often exhibit greater mortality of canopy and emergent trees (Kapos 1989, Williams-Linera 1990, Oosterhoorn and Kappelle 2000, Laurance et al. 2002), inhibition of seedling and sapling regeneration at forest edges (Benitez-Malvido 1998, Gascon et al. 2000), and increased abundance of lianas and disturbance-adapted, light-demanding, and abiotically dispersed trees near the forest edges (Oliveira-Filho et al. 1997, Laurance et al. 1998, 2002, 2006, Oosterhoorn and Kappelle 2000). Reduced regeneration and increased mortality of native vegetation in tropical forest fragments may be caused by a combination of microclimate changes such as increased air temperature, reduced humidity, and greater wind damage and light exposure, or by changes to fire regimes,

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which may reduce fragment areas over time from the edges inward (Gascon et al. 2000, Laurance et al. 2002, D'Angelo et al. 2004). Fragmentation may result in losses of carbon (C) stored in biomass because of higher rates of tree mortality coupled with changes in plant community composition, especially when lianas and pioneer species with low wood density replace slow-growing old-growth trees with high wood density (Laurance et al. 2002, 2006, 2007), leading to more flammable fuel (Brando et al. 2012). Tree species diversity is often reduced in upland forest fragments (Turner and Corlett 1996, Turner 1996, Terborgh et al. 2001, Laurance et al. 2002), yet some forest fragments isolated more than 100 years ago in the Brazilian Atlantic Forest still maintain high species diversity (Higuchi et al. 2008). The degree or intensity of past disturbance (Oliveira-Filho et al. 1997) and the physical arrangement, particularly the edge:area ratio, of forest fragments (Kapos et al. 1993, Laurance et al. 1998, Chambers et al. 2007) can have an important influence on the extent of alteration of forest properties. Additionally, some fragments and forest edges have shown decreasing fragmentation and edge effects over time as vegetation regrew and the forest edge filled in (Oliveira-Filho et al. 1997, Didham and Lawton 1999, Laurance et al. 2002), the presence of pioneer and light-demanding species decreased over time (Higuchi et al. 2008), and recruitment exceeded mortality, suggesting recovery in very old fragments (Oliveira-Filho et al. 1997).

In some tropical landscapes, forest fragments also exist as patches of forest left along stream channels. Increasingly important in areas of cropland expansion, these are in some cases mandated by land-use regulations. Compared to forest fragments in upland regions, we know much less about the dynamics of these altered riparian forests. Because the latter are typically thin strips with high edge:area ratios, changes to both forest microclimate and tree species composition and dynamics may be pronounced, and they are often highly altered and degraded (Capon et al. 2013, Stromberg et al. 2013). As the configuration and size of a fragment can influence the degree of change following fragmentation, the width of the riparian buffer left behind in altered landscapes may similarly influence changes in forest structure and composition. However, there is some evidence that riparian ecosystems may be more resilient than other systems because of their inherently heterogeneous environmental conditions, which include alternating periods of wet and dry conditions. Understanding the fate of tropical riparian forests in increasingly fragmented landscapes is important because these forests are highly valued for providing critical ecosystem services, including refugia for plant and animal species in aquatic, semi-aquatic, and terrestrial areas, and protecting stream resources by maintaining stream temperature and reducing erosion of sediments and nutrients (Meave et al. 1991, Naiman et al. 2005, Malhi et al. 2008).

Altered riparian forests are now common in agricultural landscapes of the southern Amazon and throughout

much of Brazil (Lima and Gascon 1999, Lees and Peres 2008, Macedo et al. 2013). This is because the Brazilian Forest Code mandates that land clearing practices leave standing at least 30 m of forest on both sides of streams less than 10 m wide to "conserve hydrological functions, prevent soil erosion, support frontier defence, guarantee public health, protect sites of natural beauty and provide protection for rare native species of flora and fauna" (Stickler et al. 2013). The Brazilian state of Mato Grosso has one of the world's highest rates of deforestation (DeFries et al. 2008) and is now the Amazon's biggest and fastest-growing agricultural frontier (Brando et al. 2013). Most of the land in Mato Grosso currently being used for agriculture was cleared first for pasture in the 1980s and converted to intensive soybean (*Glycine max*) cultivation after 2000 (Brando et al. 2013, Galford et al. 2013, Macedo et al. 2013). The total area in mechanized agriculture in Mato Grosso almost doubled in the decade from 2001 to 2011, growing from 38 850 to 69 421 km² (VanWey et al. 2013). Understanding the ability of altered riparian forests to provide ecosystem services in this agricultural landscape will be increasingly important as these patterns of land conversion continue.

The altered riparian forests of the southern Amazon may experience similar microclimatic shifts to those in fragments of upland tropical forests, but they differ in several other ways that may be important determinants of forest dynamics. They are long, thin strips surrounded on three sides by cleared land but connected to larger areas of intact forest further downstream. In addition, lower evapotranspiration in cropland results in more water reaching riparian zones and small stream channels in agricultural watersheds (Brown et al. 2005, Gordon et al. 2008, Hayhoe et al. 2011, Neill et al. 2013). This may influence groundwater and soil moisture conditions both in the riparian forest and in adjacent agricultural fields. Therefore, trees in these altered riparian areas may have greater access to soil water, which could compensate for greater water losses through transpiration caused by hotter and drier air conditions, and increase fire resistance. Alternatively, this higher water table could cause additional stress if the roots are inundated for long time periods. It is also possible that altered riparian forests in agricultural landscapes are resistant to change and similar in some ways to streamside or gallery forests that exist as natural fragments in drier landscapes, although the mechanism of isolation and time since isolation certainly differ. Studies in Belize and Venezuela indicated that gallery forests contain high tree species densities and rates of tree growth and turnover similar to those in continuous forests (Meave et al. 1991, MacDougall and Kellman 1992, Kellman et al. 1998).

We studied riparian forests in the Brazilian state of Mato Grosso in the southern Amazon to see if they respond similarly to upland forest fragments or naturally isolated gallery forests because they share characteristics with both. We compared riparian forests surrounded by agricultural cropland with riparian



FIG. 1. Map of the Fazenda Tanguro farm boundaries (Mato Grosso, Brazil) with altered (surrounded by soybeans; *Glycine max*) and intact (surrounded by forest) riparian forest transect locations. The background image is a Landsat 5 TM false color satellite image (bands 5, 4, and 3) from June 2011. The insets show the study design of vegetation analysis in altered riparian forests: plots (5 × 10 m; for trees) and subplots within the plots (1 × 1 m; for herbaceous cover). Intact riparian forests were sampled similarly, with transect lengths mirroring those found in the medium width (W2; 185–210 m wide) altered riparian zones.

forests within large areas of remaining intact tropical forest to examine how fragmentation of riparian forest influences forest vegetation dynamics and ecosystem services including C storage and biodiversity. We addressed the following questions: (Question 1) Do altered riparian forests have altered microclimates, including hotter and drier conditions, and are changes to microclimate greatest near forest edges? (Question 2) Have altered riparian forests degraded over time through loss of large trees and biomass, reduced tree regeneration, and decreased species richness? (Question 3) Are changes to altered riparian forest structure greater in narrower compared with wider forest remnants? (Question 4) Has increased water availability caused by a higher water table buffered altered riparian forests against the microclimatic changes typically associated with fragmentation?

This work, particularly empirical information derived from Question 3, can inform policy decisions regarding forest management practices and mandated riparian buffer width in Brazil.

METHODS

Site description

Fazenda Tanguro is an 800-km² soybean farm in the Brazilian state of Mato Grosso (13°04′35.39″ S,

52°23′08.85″ W). The mean annual temperature is 25°C and mean annual precipitation from 2005 to 2011 was 1770 mm/yr (Rocha et al. 2013). The region experiences a distinct dry season from May to August, when rainfall is <10 mm/month (Rocha et al. 2013). Today, 50% of the ranch remains in closed-canopy evergreen forests intermediate in stature between the more humid rain forests to the north and Cerrado (Brazilian savanna) vegetation to the south (Ivanauskas et al. 2004, Balch et al. 2008). The rest of the area on Fazenda Tanguro was deforested for pasture in the early 1980s. During forest clearing, some riparian buffers surrounding streams were left in place. Impoundments were also constructed on headwater streams throughout the region to provide water for cattle (Macedo et al. 2013). To initiate soybean cultivation beginning in 2003, remaining woody vegetation was piled into rows and burned and the soil was tilled, after which soybeans were planted and maintained using no-till practices (Riskin et al. 2013).

Experimental design

We studied riparian forests along four headwater streams flowing through soybean fields (altered riparian forests), and four streams flowing through intact forest (Fig. 1). We use the term “edge” to mean the forest fragment edge adjacent to the soybean field, not the less-

pronounced forest edge that exists along the stream. For each of the streams surrounded by soybeans, we created three transects perpendicular to the stream in the remaining riparian vegetation at three forest widths: narrow (W1; 75–90 m wide from edge to edge), medium (W2; 185–210 m), and wide (W3; 210–325 m). The three riparian forest widths were included to look for the presence of a threshold (Question 3) below or above which riparian forest properties change to inform management decisions on mandated riparian widths. All three of these width classes exceed the width mandated by the Brazilian Forest Code (30 m on both sides of the stream). The altered riparian forests were asymmetrical; the distance from the edge of the riparian vegetation to the stream was not equal on the two sides of the stream. All transects in altered riparian forests were at least 200 m downstream from impoundments to limit their effect on riparian vegetation. Riparian forest plots showed no sign of previous logging as indicated by stumps or other signs beyond the current maintenance of farm-field edges.

We mirrored the design of the altered riparian forest transects in the intact riparian forests. We established four transects that crossed similar-sized streams (2.1–5.7 and 2.7–4.7 m wide in intact and altered forests, respectively) and had the same length as the transects in the four W2 altered riparian forests.

Along each of the 16 transects, we sampled the vegetation in six 5 × 10 m plots (300 m²/transect) to characterize stream, mid-riparian zone (mid), and edge vegetation (Fig. 1). Several smaller plots were chosen as opposed to one larger plot because we expected variation in both vegetation (Kellman et al. 1998) and drivers of change (e.g., altered microclimate) within riparian forests, with vegetation differences most pronounced at forest edges (Question 1). This plot size and configuration maximized the available width of altered riparian forests while keeping plot size consistent among sites at different riparian widths. Plot length was constricted by (1) meandering streams and riparian buffer vegetation that followed these contours, (2) maintaining a minimum distance of 200 m from each of the impoundments, and (3) maintaining a minimum distance of 0.5 km between transects to discretize sites among the three width categories. Each transect had a complete set of the plot locations (edge, mid, and stream) on each side of the stream (Fig. 1). Because there was no comparable edge in intact riparian forests, the plots were located at distances from the stream such that they replicated the distances to the stream, mid, and edge in the W2 altered riparian forest transects. In addition to the categorical parameters of edge, mid, and stream, we measured the distance to the stream and distance to the nearest edge to use as continuous explanatory variables. The distance of each plot center to the nearest edge (altered riparian forests only) or to the stream was measured in the field.

We counted seedlings (<5 cm diameter at breast height [dbh] and <30 cm height and large enough to be seen by the naked eye), saplings (<5 cm dbh and ≥30 cm height), and lianas and estimated percent cover of grass, forbs, and ferns in five 1-m² subplots arrayed diagonally across each of the larger vegetation plots (Fig. 1). We measured all live and dead woody plants (including trees, lianas, and palms) ≥5 cm dbh in each 5 × 10 m plot (Question 2). To confirm dead vs. living trees, the bark was cut and examined for water flowing in the xylem in trees suspected to be dead. To calculate the biomass of each tree, we applied an allometric equation from Chave et al. (2005) developed for tropical moist forests with a pronounced dry season

$$\ln(\text{AGB}) = a + b \times \ln(\text{dbh}) + \ln(\rho)$$

incorporating aboveground biomass (in kg; AGB), dbh (in cm), and wood specific gravity (ρ ; in g/cm³); a and b are constants for a tropical moist forest equal to -1.864 and 2.608 , respectively. We chose the wood mean specific gravity for the site (Mato Grosso, Brazil) to be 0.61 g/cm^3 , based on Carvalho et al. (2001). To calculate the aboveground biomass of each palm, we used an equation from Goodman et al. (2013)

$$\ln(\text{AGB}) = -3.3488 + 2.7483 \times \ln(\text{dbh}).$$

To calculate the aboveground biomass of each liana, we used an equation from Gehring et al. (2004)

$$\ln(\text{AGB}) = -7.114 + 2.276 \times \ln(D)$$

where D is diameter at 30 cm height (in mm). To calculate the liana diameter at 30 cm height, we followed the equation from Gehring et al. (2004)

$$D = 1.235\text{dbh} + 0.002\text{dbh}^2.$$

We calculated C content of trees, palms, and lianas as 50% of the biomass of each woody plant. We calculated the basal area (cross-sectional area) of all large woody plants with the equation

$$\text{BA} = \pi \left(\frac{\text{dbh}}{2} \right)^2$$

where BA is the basal area. We re-censused trees one year after initial plot establishment and calculated annual mortality as the number of newly dead trees per plot divided by the total number of trees per plot. We assayed canopy cover using leaf area index (LAI) measurements from a LAI-2000 plant canopy analyzer (LI-COR, Lincoln, Nebraska, USA) every 10 m along each transect in the intact and W2 altered riparian forests only.

We identified plants ≥5 cm dbh (including trees, palms, and lianas) to species, when possible. The flora of the region is well known, and local botanists from the Instituto de Pesquisa Ambiental da Amazônia (IPAM) identified the trees. If the species was unknown, trees were identified to the genus level. If the genus was unknown, trees were included in an “unknown”

category that encompassed 41 of 862 or 4.75% of the total number of trees in all plots. Unknown trees were excluded from compositional analyses, but were included in structural analyses (size distribution, biomass, etc.). To reduce the influence of extremely rare species, if there was only one tree of a known species found in any of the plots (i.e., singletons) we removed that species from the compositional analyses (Toti et al. 2000). As a metric of a species' contribution to the community, we calculated the importance value index (IVI) for each species at each site using the following equation:

$$IVI = RBA + RD + RF$$

where IVI is the importance value index, RBA is the relative basal area ((basal area of each species/total basal area of all species) \times 100), RD is the relative density ((number of individuals per species per plot/total number of individuals of all species per plot) \times 100), and RF is the relative frequency ((number of occurrences of each species/number of occurrences of all species combined) \times 100)), following Dangol and Shivakoti (2001) and Bautista et al. (2014).

We monitored air temperature, relative humidity, and light (wet season only) simultaneously along a W2 altered riparian forests and its paired intact riparian forest transect using HOBO Tidbit v2 water temperature data loggers, HOBO U23 Pro v2 temperature/relative humidity data loggers, and HOBO Pendant temperature/light data loggers (Onset, Bourne, Massachusetts, USA). We collected data from three different transect pairs over the course of three weeks in the dry season (18 June–9 July 2013, measured every 30 min for six continuous days in each altered–intact pair), and for one transect pair over the course of one week in the rainy season (8–14 March 2013, measured every 30 min). We placed loggers roughly every 20 m along each transect, depending on the total transect length. We calculated vapor pressure deficit (VPD; in Pa) with the following equation

$$VPD = \left(1 - \frac{RH}{100}\right) \times SVP$$

where RH is the relative humidity (%) and SVP is the saturated vapor pressure (Pa). SVP was calculated from

$$SVP = 610.7 \times 10^{(7.5T/237.3+T)}$$

where T is the temperature ($^{\circ}\text{C}$; Monteith and Unsworth 1990).

To measure water table depth along the transects, we installed four to six wells along each intact and W2 altered riparian forest transect. We placed HOBO U20 water level loggers in wells of each transect pair ($n =$ three pairs) for roughly one-week intervals in the dry season (18 June–9 July 2013), when we expected the differences in water table height between forest types to be greatest. We determined the change in relative elevation along the transect using traditional surveying methods using an AT-G2 automatic level, tripod, and surveyor's rod (Topcon Positioning,

Madrid, Spain). We used pressure data from the water level loggers and converted it to the water depth below the soil surface. To map a profile of the water table from well to well along each transect, we subtracted the depth of the water table below the soil surface from the well's relative elevation (relative to the most upland well in the transect).

Statistical analysis

All statistical comparisons were done in R version 3.0.1 (R Core Team 2013), and we assessed significance at $P < 0.05$. All variables were tested for normality; if the data did not approach normality, a suite of transformations were employed (log, square root, etc.) and if normality was still not achieved, nonparametric statistical tests were used.

We compared differences in temperature, relative humidity, VPD, and light at forest edges (0 m along the transect) in W2 altered and intact riparian forests with a Wilcoxon signed rank test. We analyzed the water table depth in paired wells in intact and W2 altered riparian sites with a paired t test.

We used a G test of independence with a row by column ($R \times C$) contingency table to analyze whether counts of seedlings and saplings differed among forest types and locations (Sokal and Rohlf 1995). We also analyzed counts of seedlings, saplings, lianas, and live and dead trees among forest types (intact riparian forest and W1, W2, and W3 altered riparian forests) and locations (edge, mid, stream) using generalized linear models with a Poisson distribution and HSD tests (R package agricolae; Mendiburu 2014) when we found significant differences among groups (Kindt and Coe 2005). We used a Kruskal-Wallis rank sum test to analyze percent grass cover among forest types (intact, W1, W2, W3). We analyzed mortality among forest types and locations using Kruskal-Wallis rank sum tests.

In addition to analyzing plots in discrete categories of location (edge, mid, stream), we compared counts of seedlings, saplings, lianas, and live and dead trees in altered riparian forests to the distance from the stream and distance from the nearest edge using generalized linear models with a Poisson distribution (Kindt and Coe 2005). We compared mean tree dbh to the distance from the stream and distance from the nearest edge using multiple regression.

To compare size distributions of all trees among forest types (intact vs. W1, intact vs. W2, and intact vs. W3), we used Fisher's exact tests (Kindt and Coe 2005). We also compared tree size distributions, with binned tree diameters (e.g., 5–10 cm, 10–15 cm), of all four forest types (intact, W1, W2, W3) simultaneously using a G test of independence (Sokal and Rohlf 1995).

We analyzed aboveground large woody plant C stocks using ANOVA on \log_{10} -transformed data. We used a t test to compare LAI along transects in intact and altered (W2 only) riparian transects and linear regression to compare LAI and distance to the nearest edge.

For analysis of species composition and diversity, we excluded the mid locations of each transect because mid

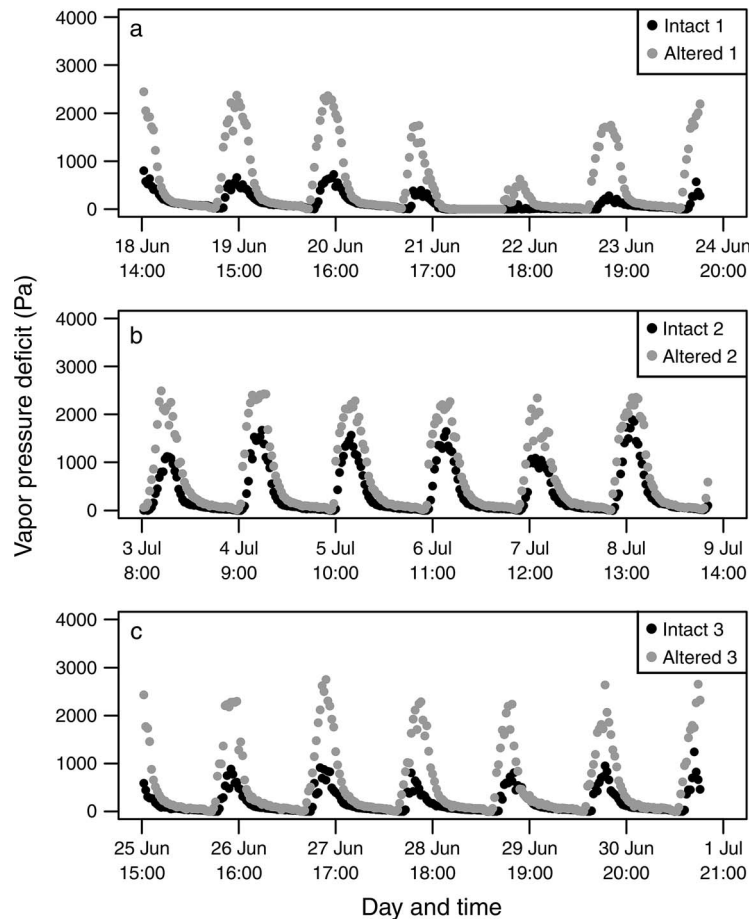


FIG. 2. Vapor pressure deficit (Pa) during the dry season at forest edges in Fazenda Tanguro (0 m along transect; at forest edge) of paired sites: (a) intact 1 and altered 1, 18–24 June 2013; (b) intact 2 and altered 2, 3–9 July 2013; (c) intact 3 and altered 3, 25 June–1 July 2013.

plots ranged from well-drained uplands to waterlogged near-stream zones, depending on the configuration of the riparian forest and the location of the stream within the relatively flat area on either side of the stream channel. In contrast, the edge and stream locations were always upland or adjacent to the stream channel, respectively. To examine the effect of forest type and plot location on species composition, we grouped the two sides of each stream while keeping each stream separate. Thus for all analyses of species composition and diversity, we analyzed a total of 32 sites: 16 adjacent to a stream, and 16 at the forest edge (or the same distance from the stream in intact forest as one of the edges in the altered riparian forest).

To analyze species composition of all large woody plants with $\text{dbh} \geq 5$ cm, we selected a similarity metric, Kulczynski distance, and the constrained ordination method, principal coordinates analysis (PCoA) with Bray-Curtis distance method, in the BiodiversityR (Kindt and Coe 2005) and Rcmdr (Fox 2005) packages to plot differences in species abundances among sites (Kindt and Coe 2005). Both the Kulczynski and the

Bray-Curtis distances are more appropriate for ecological data than metrics using Euclidian distances (e.g., principal components analysis; Faith et al. 1987, Kindt and Coe 2005). To make the PCoA graph, we used the ggplot2 (Wilson 2009) package features.

To study large woody plant species diversity, we calculated the species richness, Shannon diversity index, Simpson index, and inverse Simpson index for each forest type (intact, W1, W2, W3).

RESULTS

Microclimate and hydrology

During the dry season, edges of altered riparian forests were significantly hotter and had significantly lower relative humidity (RH) than edges of intact riparian forests (mean values of 22.6°C vs. 21.2°C and 92.9% RH vs. 83.8% RH for altered and intact, respectively). Mean VPD was significantly higher at altered riparian forests edges than intact riparian forests edges in the dry season (606 Pa compared to 226 Pa), with the greatest differences just after midday (Fig. 2). During the dry season, the water table was significantly

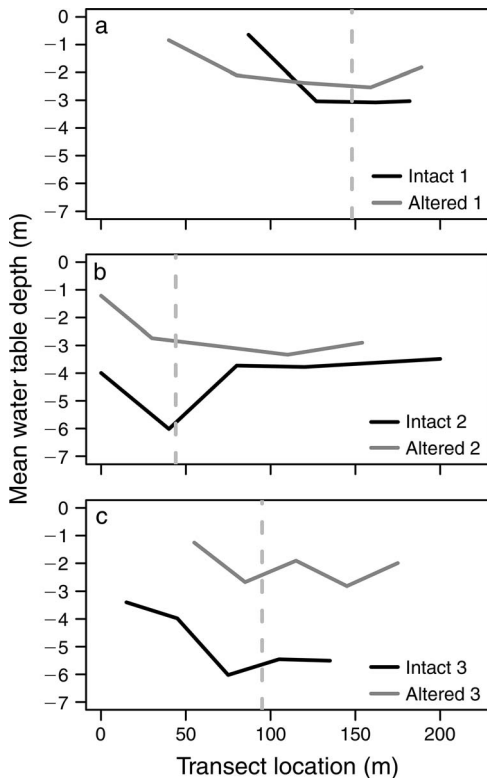


FIG. 3. Mean adjusted water table depth (m belowground) relative to the starting transect elevation in wells for altered and intact paired sites. (a) Intact 1 and altered 1; (b) intact 2 and altered 2; (c) intact 3 and altered 3. The light gray dashed vertical line represents the stream location along each transect. Data shown are mean values over the entire ~1-week interval at each site pair in the dry season (18 June–9 July 2013).

closer to the soil surface in altered than in intact riparian forests, sometimes by several meters (Fig. 3).

During the wet season, the temperature at the edges of intact vs. altered riparian forests did not vary signifi-

cantly (mean values of 25.5°C and 26.1°C for intact and altered riparian forest edges, respectively). We were not able to collect RH data from forest edges during the wet season and therefore cannot calculate VPD during this time. There was significantly more light (as measured in lux) at the edges of altered riparian forests than at edges of intact riparian forests during the wet season (mean values of 6490 lx for altered riparian forests and 3200 lx for intact riparian forests).

Seedlings and saplings

There were significantly fewer seedlings in narrow (W1), medium (W2), and wide (W3) altered riparian forests compared with intact riparian forests (Table 1). These differences in seedling numbers were most pronounced among edge plots (Table 2). There were significantly fewer saplings in W1 and W2 altered riparian forests compared with W3 altered and intact riparian forests (Table 1). Saplings were significantly less abundant in W1 and W2 sites in both edge and stream plots (Table 2). The number of seedlings and saplings increased with increasing distance from the stream in altered riparian forests (Table 3). There was no difference in counts of seedlings and saplings across all forest type (intact, W1, W2, W3) and location (stream, mid, edge) simultaneous combinations (data not shown).

Forest structure and functional composition

LAI at forest edges (0 m along the transect) did not differ between intact and altered riparian forests (4.5 ± 0.4 for intact and 4.4 ± 0.5 for [W2] altered riparian forests; all means shown \pm SE), but was significantly lower along entire transects in altered than intact riparian forests (Fig. 4). There was more variation in LAI among streams in altered than in intact riparian forests (Fig. 4). LAI was positively and significantly related to the distance from the nearest edge (data not shown).

TABLE 1. Descriptive statistics for large woody plants ≥ 5 cm diameter at breast height (dbh), small plants < 5 cm dbh, and grass cover at Fazenda Tanguro, an 800-km² soybean farm in Mato Grosso, Brazil.

Vegetation component	Units	Intact forest	Altered forest		
			W1	W2	W3
Plots					
All large woody plants	no./50 m ²	8.1 ^a (0.7)	9.1 ^a (0.7)	8.4 ^a (0.6)	9.3 ^a (0.7)
Dead woody plants	no./50 m ²	0.7 ^a (0.2)	0.8 ^a (0.2)	0.4 ^a (0.2)	0.6 ^a (0.2)
Trees only	no./50 m ²	7.1 ^c (0.5)	8.8 ^{ab} (0.7)	8.1 ^b (0.6)	9.0 ^a (0.8)
Palms only	no./50 m ²	0.6 ^a (0.4)†	0.0 ^a (0.0)†	0.3 ^a (0.2)†	0.2 ^a (0.1)†
Large lianas	no./50 m ²	0.4 ^a (0.1)†	0.4 ^a (0.1)†	0.0 ^a (0.0)†	0.2 ^a (0.1)†
Subplots					
Seedlings	no./m ²	21.2 ^a (4.0)	12.6 ^c (1.6)	13.1 ^c (1.9)	15.7 ^b (3.6)
Saplings	no./m ²	5.7 ^a (0.5)	2.4 ^b (0.2)	2.5 ^b (0.4)	5.3 ^a (0.8)
Small lianas	no./m ²	0.8 ^b (0.1)	1.6 ^{ab} (0.4)	2.0 ^a (0.4)	1.9 ^a (0.4)
Grass	% cover	2.8 ^a (1.0)	6.5 ^a (3.0)	9.4 ^a (2.3)	8.1 ^a (2.5)

Notes: Means are shown with standard error in parentheses. Significant differences in mean values are indicated by different superscripted letters. Plots were 50 m², subplots were 1 m². Forest types were intact riparian forest, and narrow (W1; 75–90 m wide from edge to edge), medium (W2; 185–210 m), and wide (W3; 210–325 m) altered riparian forest.

† A significant difference was found among means, but pairwise post hoc comparisons did not find a difference among groups.

TABLE 2. Number of seedlings and saplings.

Groups	Intact	W1	W2	W3	Deviance explained
Seedlings					
Edge	31.1 ^a (10.7)	11.3 ^c (1.7)	16.5 ^b (3.7)	26.5 ^a (9.3)	21.3%
Mid	22.0 ^a (3.5)	15.1 ^b (2.7)	15.0 ^b (3.8)	13.5 ^b (3.6)	10.8%
Stream	10.5 ^{ab} (2.1)	11.9 ^a (3.7)	8.0 ^{bc} (1.6)	7.2 ^c (1.3)	10.1%
Saplings					
Edge	6.9 ^a (3.2)	2.3 ^b (0.3)	2.7 ^b (0.8)	5.3 ^a (1.1)	50%
Mid	6.1 ^a (1.1)	2.8 ^b (0.5)	3.2 ^b (0.9)	5.8 ^a (2.1)	21.3%
Stream	6.2 ^a (0.8)	2.0 ^b (0.2)	1.7 ^b (0.2)	4.8 ^a (1.1)	41.3%

Notes: Means are shown with standard error in parentheses. When analyzed among all groups (forest type and location) at once, there were no significant differences among groups. Significant differences within edge, mid, or stream plots only are indicated by different superscripted letters.

Of the 862 total large woody plants (all trees, palms, and lianas ≥ 5 cm dbh) in all plots, 63.9% were in the 5–10 cm dbh size class and only 1.7% were greater than 40 cm dbh. The size distribution of large woody plants (Fig. 5) did not vary significantly among altered and intact riparian forests. The number of large woody plants per plot did not vary significantly with forest type (intact, W1, W2, W3; Table 1) or with location (edge, mid, stream; data not shown). The number of dead large woody plants did not differ between intact and altered riparian forests (Table 1), and among altered sites only, dead large woody plant abundance was not related to distance from nearest forest edge (Table 3). Annual mortality did not vary significantly among forest types ($3.9\% \pm 1.7\%$, $4.2\% \pm 1.7\%$, $6.5\% \pm 3.4\%$, and $2.7\% \pm 1.1\%$ for intact, W1, W2, and W3, respectively). Within the large woody plants, there were significantly fewer trees in intact than altered riparian forests (Table 1). The number of trees did not vary with location (data not shown). Poisson regression indicated significant differences in the number of large lianas and palms among forest types, but pairwise comparisons did not allow us to determine which groups differed. Numerically, large lianas were most abundant in intact and W1 and least abundant in W2 altered riparian forests, and palms were most abundant in intact and least abundant in W1

altered riparian forests (Table 1). There was also a significant difference in the number of large lianas and palms among locations along the transect, although pairwise comparisons did not show differences among the edge, mid, and stream groups (mean large liana counts of 0.1 ± 0.1 , 0.4 ± 0.1 , and 0.2 ± 0.1 for edge, mid, and stream, respectively; mean palm counts of 0.0 ± 0.0 , 0.4 ± 0.3 , and 0.4 ± 0.2 for edge, mid, and stream, respectively). Large woody plant biomass and C content did not differ significantly among forest types; the mean aboveground C content was 13.2, 8.3, 15.3, and 15.8 kg C/m² for intact, W1, W2, and W3, respectively.

There were significantly more small lianas in the wider altered riparian sites (W2 and W3) than in intact riparian sites, but the number of small lianas in narrow altered riparian (W1) sites did not differ significantly from any of the other sites (Table 1). Small liana abundance was significantly and negatively related to the distance from stream in altered riparian forests (Table 3). Grass cover was low in all plots and did not vary significantly among forest types (Table 1). Grass cover did vary significantly with location: grass cover was significantly lower in edge plots than in mid or stream plots ($0.5\% \pm 0.2\%$, $9.7\% \pm 1.3\%$, and $9.9\% \pm 2.4\%$ for edge, mid, and stream, respectively).

TABLE 3. Regression models between number of large woody plants, dead woody plants, small lianas, seedlings, saplings, and mean woody plant size (for woody plants ≥ 5 cm dbh) and distance from stream (dst) and nearest edge (dne) for altered riparian forests only.

Model type and dependent variable	Explanatory variable				Deviance explained by model
	First	<i>P</i>	Second	<i>P</i>	
Poisson					
No. large woody plants	dne (–)	0.83	dst	0.89	0.1%
No. dead woody plants	dne	0.28	dst	0.77	2.0%
Mean no. small lianas	dne (–)	0.13	dst (–)	<0.001	20.8%
Mean no. seedlings	dne (+)	0.15	dst (+)	<0.001	21.4%
Mean no. saplings	dne (+)	0.22	dst (+)	0.001	6.5%
Multiple					
log(mean dbh)	log(dne)	0.92	log(dst)	0.43	1.0%

Notes: Significant relationships ($P < 0.05$) are indicated in bold and the direction of the relationship (+) or (–) is indicated following the explanatory variable. The distance to nearest edge or stream was measured in the field.

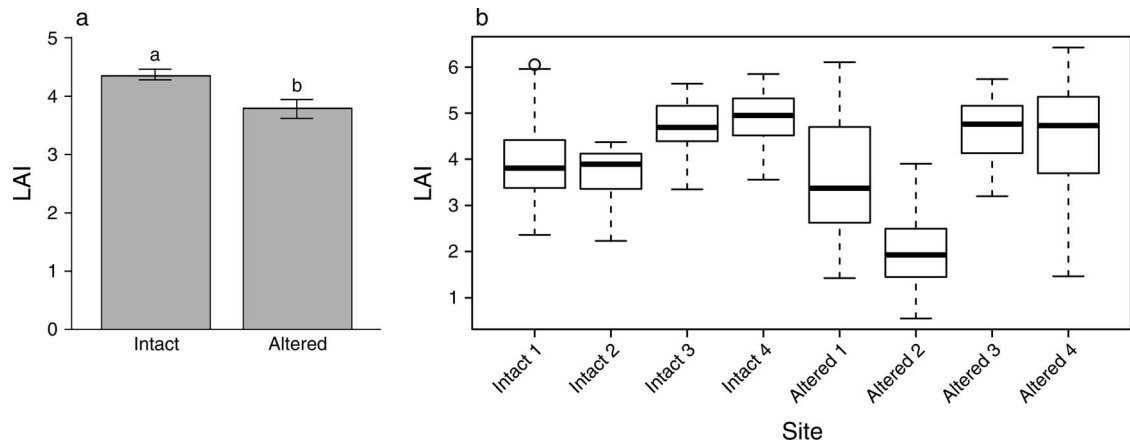


FIG. 4. Leaf area index (LAI; m^2 leaf area/ m^2 ground area) in intact and altered riparian sites. (a) Mean and standard error across all intact and altered sites (differences significant at $P < 0.05$ marked with different lowercase letters), and (b) boxplots of LAI at individual sites. The bold line within each box is the median value for that site. The box endpoints are the lower (25%) and upper (75%) quartiles, the whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box, and the circles outside the whiskers are outliers. Measurements were taken every 10 m along the transects.

Tree species composition and diversity

Among all plots, there were 110 known species of large woody plants (trees, palms, and lianas ≥ 5 cm dbh). The species with the highest IVIs among all altered riparian forests were (ranked from the most important) *Nectandra cuspidata*, *Maprounea guianensis*, *Tapirira guianensis*, *Qualea witrockii*, *Protium spruceanum*, and *Inga heterophylla* (Appendix: Table A1). The species with the highest IVIs in intact riparian forests were *Miconia pyrifolia*, *Protium guianense*, *Miconia* sp., *P. spruceanum*, *Xylopia amazonica*, and *Euterpe* sp. (Appendix: Table A1). Intact riparian

forests shared one of the six most important species with all altered riparian forests, two species with the W2 and W3 forests, and no species with the W1 forests (Appendix: Table A1).

For all woody plants with dbh ≥ 5 cm, the Kulczynski distance metric indicated significant differences among forest types ($P = 0.001$), locations ($P = 0.004$), and individual streams ($P = 0.001$). The first two dimensions of the PCoA analysis among the 32 sites explained 44% of the variance and separated the intact riparian forests from all altered riparian forests with no overlap (Fig. 6). Species richness was highest in W2 altered riparian

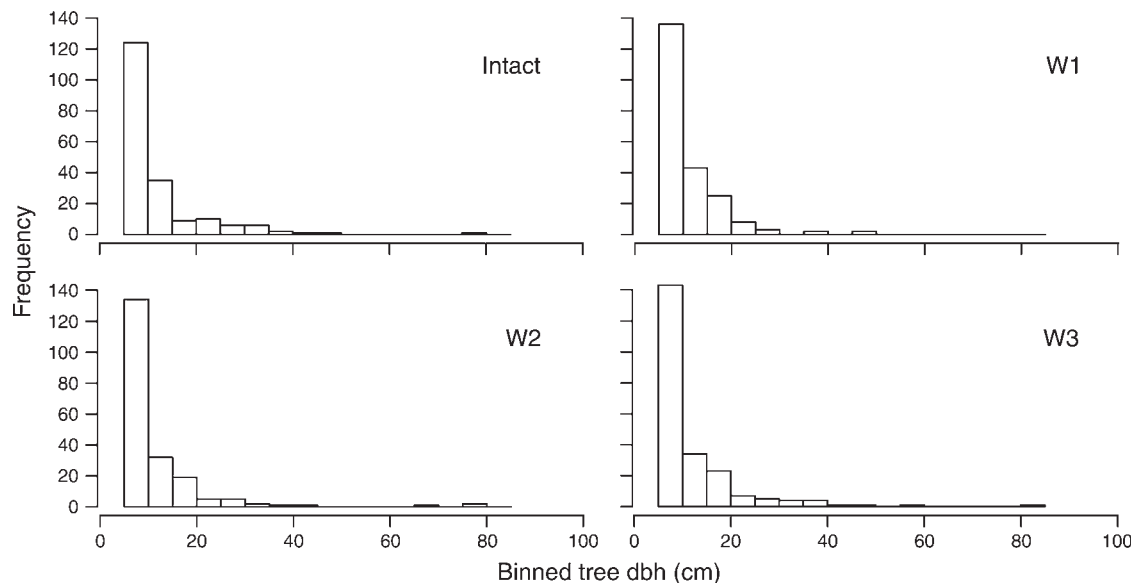


FIG. 5. The number of live trees (frequency) in binned size classes (diameter at breast height, dbh) in intact and narrow (W1; 75–90 m wide from edge to edge), medium (W2; 185–210 m), and wide (W3; 210–325 m) altered riparian forests plots.

forests, but three diversity indices, the Shannon diversity index, the Simpson diversity index, and the inverse Simpson index, found higher diversity in intact than all altered riparian sites (Table 4).

DISCUSSION

Hotter and drier understories in altered compared to intact riparian forests, which produced conditions conducive to greater plant water loss from leaves during the dry season (Fig. 2), were consistent with the findings of other studies that compared fragmented and intact upland forests (Kapos 1989, Williams-Linera 1990, Murcia 1995, Gascon et al. 2000, Laurance et al. 2002). Altered microclimatic conditions at forest edges can penetrate up to 100 m toward the forest interior (Laurance et al. 2002). We found these differences permeated the entirety of the forest fragment (185–210 m wide) in the dry season. Changes to microclimate of this magnitude are associated with plant stress and have been linked to higher tree mortality in other forest fragments (Kapos 1989, Benitez-Malvido 1998, Laurance et al. 2002) in plants lacking drought-tolerant characteristics.

Reduced abundances of seedlings and saplings in altered riparian fragments (Tables 1 and 2) were also consistent with findings in upland forest fragments (Benitez-Malvido 1998, Gascon et al. 2000, Santo-Silva et al. 2012). The mechanisms that caused reduced seedling and sapling abundance are not known. Greater reduction in seedling (edge locations only) and sapling (all locations) abundances in narrow (W1) than medium (W2) and in medium than wide (W3) altered riparian zones may indicate a tolerance threshold (Question 3) beyond which the establishment of seedlings or survival of saplings is reduced. Inhibited regeneration may have consequences for the future of altered riparian zones, but it remains to be seen if reductions in seedling and sapling abundance will propagate to larger size classes of trees. Because tree longevity in tropical forests is high, reduced seedling and sapling abundance suggests the possibility of an extinction debt, or inevitable future extinctions caused by past events (Magnago et al. 2013).

The size distribution and number of all standing large woody plants, dead large woody plants, annual mortality, and biomass and C storage in altered and intact riparian forests were similar. The lack of significant differences in the structure of the large woody plant community 30 years after forest clearing contrasts with increases in tree mortality and reduced tree biomass associated with fragmentation and edge creation in upland areas (Kapos 1989, Williams-Linera 1990, Laurance et al. 1998, 2002). It was more consistent with results from naturally isolated gallery forests (Meave et al. 1991, MacDougall and Kellman 1992, Kellman et al. 1998). Mean LAI was lower in altered riparian forests than intact riparian forests, but this result was driven by one large open patch along one stream (altered stream 2; Fig. 4). Thus, the pattern of more and larger gaps in

forest canopies in forest fragments and near forest edges (Williams-Linera 1990, Kapos et al. 1993, Laurance et al. 1998, Oosterhoorn and Kappelle 2000, Chambers et al. 2007) was only weakly supported at our sites.

Increased small liana abundance in wider (W2 and W3) altered riparian forests (Table 1) is consistent with some previous studies in upland forest fragments (Laurance et al. 2002, 2007), but the pattern did not hold for the narrow (W1) altered riparian forests or for larger (≥ 5 cm dbh) lianas. Williams-Linera (1990) found increased abundance of large (≥ 5 cm dbh), but not small (< 5 cm dbh) lianas near forest edges. In fragmented forests (Laurance et al. 2002) and non-fragmented forests (Phillips et al. 2002), and among a variety of forest systems (Oliveira et al. 2013), lianas have been correlated with higher tree mortality and changes in forest structure and species composition. We found no evidence that greater abundance of small lianas affected forest structure by increasing tree mortality as found elsewhere (Laurance et al. 1998, 2002).

Original forest clearing at Fazenda Tanguro occurred in the early 1980s and land was used for cattle pasture for ~ 20 years until conversion to soybean cultivation from 2003 to 2008 (Riskin et al. 2013). It is possible that changes to forest structure took place closer to the time of initial land clearing, but that over time these effects have lessened as altered riparian forest edges fill in, as has occurred in some forest fragments (Didham and Lawton 1999, Laurance et al. 2002; but see Laurance et al. 1998). This would cause microclimate differences to lessen at forest edges. We found that LAI at riparian forest edges was not significantly different between altered and intact sites, but that microclimatic differences existed at forest edges, lending only partial support to this idea. We did not have the long-term recruitment data and relative rates of recruitment vs. mortality needed to further evaluate this possibility.

Alternatively, there are several reasons why larger woody plants in altered riparian forests may be buffered against the changes to forest structure that often result from fragmentation. A higher water table relative to the ground surface in altered riparian forests compared with intact riparian forests (Fig. 3) may alleviate some of the stress from the hotter, drier conditions and greater water loss at the leaf level experienced by plants at forest–field edges (Question 4). In some locations, mature trees near streams use primarily deep water (Dawson and Ehleringer 1991), and in some cases, access to soil water can sustain plant productivity under conditions of increased temperatures and lower humidity (Lobell and Gourdjji 2012).

It is also possible that microclimate changes on the order of those we measured have little or no influence on tree condition. Kapos (1989) found that in the rainy season, a hotter and drier microclimate near forest edges did not cause plant water deficits in understory shrubs compared with interior forest shrubs, suggesting that these plants reduced their stomatal conductance and thus controlled water loss despite microclimatic differences.

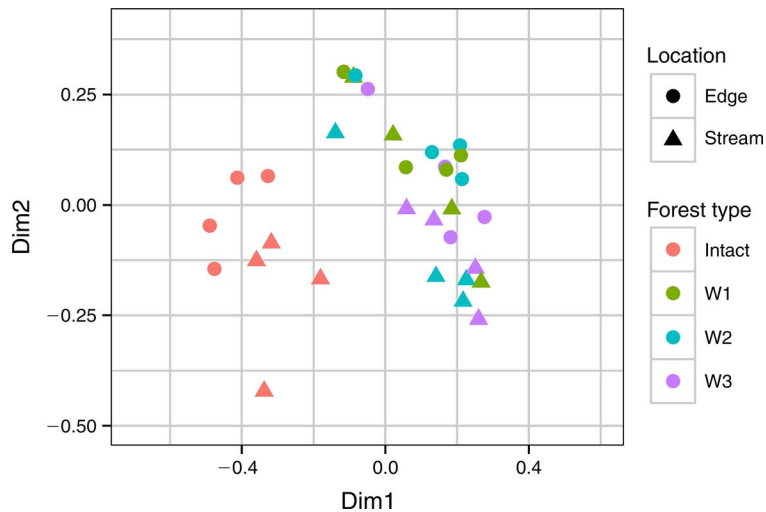


FIG. 6. Ordination graph of the first two axes (dimensions 1 and 2) of a principal coordinates analysis (PCoA) of species composition among sites based on the Bray-Curtis distance. There was a total of 32 sites: both sides of the stream were grouped together and middle locations were excluded (only stream and edge were used). Data include all trees with dbh \geq 5 cm.

The significantly higher VPD in altered riparian forests compared to intact riparian forests (Fig. 2) may not be severe enough stress to induce mortality in larger trees.

In the adjacent Cerrado, riparian forests typically exist as gallery forests along streams that persist amid a drier landscape with much less tree cover (Ratter et al. 1997, Marimon et al. 2010), similar to the gallery forests of Belize and Venezuela (Kellman et al. 1998). It may be that in the riparian forests at Fazenda Tanguro, trees are more tolerant of the microclimate changes and fluctuations caused by fragmentation because they inhabit the transition from Cerrado to tropical evergreen rain forest. Pioneer species, for example, can tolerate the hotter, drier, and higher-light conditions near forest edges, while climax and specialist species are often lost following fragmentation (Laurance et al. 1998, 2002, Gascon et al. 2000, Santo-Silva et al. 2012, Kimberley et al. 2014). The most abundant and most dominant species that we found in altered riparian forests, *N. cuspidata*, is a pioneer species common in young forests and at forest edges throughout the tropics (Condit et al. 2010). We found little overlap in the most important species (Appendix: Table A1) in altered (particularly W1 sites) compared to intact riparian forests. This suggests that edge and fragmentation effects have altered the composition of riparian forest fragments over time (Fig. 6).

This result suggests that tree species diversity and composition may be more sensitive to fragmentation

and land-use change than the number of trees, tree mortality, biomass, or C storage. Our finding of lower diversity in altered riparian forests than intact riparian forests by several metrics is consistent with reduced plant species diversity in upland tropical forest fragments (Turner 1996, Terborgh et al. 2001, Laurance et al. 2002). However, some studies have found that naturally isolated gallery forests maintain high plant species diversity (Meave et al. 1991, MacDougall and Kellman 1992), although this is likely confounded with density–diversity relationships, because a greater number of smaller stems may be found in gallery forests than in continuous forests with larger diameter trees.

Management implications

Riparian forests can play important roles in connecting and maintaining forest patches and reducing alterations to streams in expanding agricultural landscapes worldwide (Fischer et al. 2006) and land-use regulations to protect riparian forest exist in many places (Harvey et al. 2008, Stickler et al. 2013). The riparian forests at Fazenda Tanguro generally meet or exceed the minimum forest buffer width requirements mandated by the Brazil Forest Code (Soares-Filho et al. 2014). We found that these forests provide some, but not all, of the ecosystem services as their intact counterparts. For example, more than 30 years after initial forest clearing for pasture, these altered riparian forests had

TABLE 4. Diversity indices of intact and altered riparian forests.

Diversity index	Intact	W1	W2	W3
Species richness	43	38	47	35
Shannon	3.13	2.24	2.24	2.04
Simpson	0.91	0.71	0.69	0.66
Inverse Simpson	10.70	3.43	3.20	2.97

the same size distribution of large woody plants, biomass, and aboveground C storage, but had reduced tree species diversity, altered species composition, and reduced seedling and sapling abundance. Lower seedling and sapling abundance may be the most important of these changes because this could reduce long-term forest viability. Whether or not these changes are enough to warrant a reevaluation of the minimum riparian width is not clear from this study, nor are the benefits of wide riparian forests limited to the metrics we studied here.

Changes to the Brazilian Forest Code enacted in April 2012 maintained the requirement that 30-m riparian forest buffers be conserved along streams after initial forest clearing, but it lowered the width of riparian forest that must be replanted and restored in already-cleared areas to 5 m (Salomon 2011, Tollefson 2012, Macedo et al. 2013). We found that the narrowest riparian forests we studied, while complying with the 30-m width requirement for new clearing, also experienced the greatest changes to seedling and sapling abundance. This suggests that further reductions to the required width of riparian forests in new clearings and the implementation of narrow widths in cases of existing clearing will not be sufficient to avoid changes to forest regeneration.

Altered fire regimes in Amazonian upland fragments provide a positive feedback to increased tree mortality and fragment degradation (Laurance et al. 2002, 2006). There is potential for the warmer, drier climatic conditions and reduced plant water content during the dry season, coupled with more early successional species with lower wood density, to transform these altered riparian forests into more flammable systems with enhanced fire regimes (Brando et al. 2012, 2013). Conversely, the higher water table and their spatial isolation may buffer these riparian zones somewhat against increased likelihood of fire. Thus, several trajectories are conceivable with respect to future fire regimes of these altered riparian forests. Similar to naturally isolated gallery forests in Belize that rely on fire-insensitive species to persist in the landscape (Kellman et al. 1998), management of these altered riparian forests could include planting of fire-resistant species throughout riparian forests, but especially near the edges.

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: <http://dx.doi.org/10.1890/14-1740.1.sm>

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.418b0>