



Grass-dominated vegetation, not species-diverse natural savanna, replaces degraded tropical forests on the southern edge of the Amazon Basin

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ABSTRACT

Changes in land-uses, fire regimes, and climate are expected to promote savanna expansion in the Amazon Basin, but most studies that come to this conclusion fail to define “savanna” clearly or imply that natural savannas of native species will spread at the expense of forest. Given their different conservation values, we sought to differentiate between species-diverse natural savannas and other types of fire-maintained grass-dominated vegetation that replaced tropical forests between 1986 and 2005 in 22,500 km² of eastern lowland Bolivia. Analysis of Landsat TM and CBERS-2 satellite imagery revealed that, in addition to 1200 km² (7.1%) of deforestation for agriculture and planted pastures, 1420 km² (8.4%) of forest was replaced by derived savannas. Sampling in 2008 showed that natural savannas differed from forest-replacing derived savannas floristically, in soil fertility, and in fuel loads. Natural savannas typically occurred on sandy, acidic, nutrient-poor soils whereas most derived savannas were on comparatively fertile soils. Fuel loads in derived savannas were twice those of natural savannas. Natural savannas supported a diversity of grass species, whereas derived savannas were usually dominated by *Guadua paniculata* (native bamboo), *Urochloa* spp. (exotic forages), *Imperata brasiliensis* (native invasive), *Digitaria insularis* (native ruderal), or the native fire-adapted herb *Hyptis suaveolens* (Lamiaceae). Trees in derived savannas were forest species (e.g., *Anadenanthera colubrina*) and fire-tolerant palms (*Attalea* spp.), not thick-barked species characteristic of savanna environments (e.g., *Curatella americana*). In addressing tropical vegetation transitions it is clearly important to distinguish between native species-diverse ecosystems and novel derived vegetation of similar structure.

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1. Introduction

Vast areas of Amazonian forest are reportedly vulnerable to savanna expansion due to the combined effects of climate change, intensification of land-use, and fire (Uhl and Buschbacher, 1985; Cochrane et al., 1999; Laurance, 2003; Cox et al., 2004; Nepstad et al., 2008). Envisioning savannas as an alternative stable state (sensu Holling, 1973; Suding et al., 2004), various authors have posited that the positive feedbacks between deforestation, drought, tree mortality, fire, and atmospheric carbon dioxide concentrations (Nepstad et al., 2004; Golding and Betts, 2008) coupled with the grass-fire cycle (D'Antonio and Vitousek, 1992), will cause forest to switch to savanna-like scrub (Nepstad et al., 1999), savanna-like vegetation (Nepstad et al., 2008), old fields or scrub savanna (Cochrane and Schulze, 1999), or savanna (Hutyra et al., 2005;

Malhi et al., 2009). The ill-defined term, “savannization,” has been applied to the spread of natural savanna (Cavelier et al., 1998) as well as to the range of processes that degrade forest (Borhidi, 1988; Nepstad et al., 1999).

While there are reasons to expect grass-dominated fire-maintained vegetation to replace forests (Bond, 2008), it is imprecise and potentially misleading to refer to outcomes of tropical forest degradation as “savanna” (Barlow and Peres, 2008). Over past millennia, climate shifts and fire influenced the distribution, extent, and evolution of savannas around the world (Edwards et al., 2010; Bond and Parr, 2010) including those of the species-rich and highly threatened Cerrado Biome of South America (Oliviera and Marquis, 2002; Mayle et al., 2004; Simon et al., 2009). In contrast, modified fire regimes coupled with the introduction of African forage grasses in the Neotropics resulted in the creation of vast areas of physiognomic or “derived” savannas over the last century (Daubenmire, 1972; Parsons, 1972). While definitions based solely on physiognomy are useful in remote sensing and continental-scale modeling, they ignore floristics and whether the dominant species are native or exotic, naturally regenerated or planted.

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We begin this study with a definition of “savanna” as any vegetation dominated by graminoids (>25% graminoid ground cover) with an open overstory of scattered trees (<65% tree canopy cover). Our principal motive for this broad definition is that ecologists increasingly conceive of grass-dominated or “grassy vegetation” as a group, including grasslands, savannas, and woodlands (Edwards et al., 2010; Bond and Parr, 2010). Furthermore, we wanted to be inclusive of all types of vegetation that have been referred to as “savanna” (e.g., Cochrane and Schulze, 1999; Nepstad et al., 2008; Malhi et al., 2009). Importantly, we distinguish between species diverse, old-growth, “natural savannas” and forest-replacing “derived savannas” (Putz and Redford, 2010).

Species differ in a wide range of characteristics that can result in differences in ecosystem processes including responses to disturbance. For example, grass species are not all equal in their ability to co-exist with trees, to invade forest, or to drive savanna expansion (e.g., Lippincott, 2000; Platt and Gottschalk, 2001; Hoffmann et al., 2004). Among the many ways tree species differ, thick-barked savanna trees are more fire tolerant than thin-barked forest trees (Hoffmann et al., 2009). Despite evidence that not all species of the same life form are functional equivalents, climate models for the Amazon Basin consider forests to be dominated by trees and savannas to be dominated by C_4 grasses (Cox et al., 2004). As a consequence of these assumptions, the climate currently associated with savannas is assumed to be predictive of future savanna distribution (e.g., Hutyrá et al., 2005; Malhi et al., 2009). To imply that Amazonian forest will be replaced by natural savanna as the Basin dries may be wrong, at least in the short term (i.e., years to decades), because what replaces these forest may be floristically and functionally quite different from natural savanna. Indeed, to date there is little evidence that large scale natural savanna expansion is occurring (Bond, 2008).

The region of seasonally dry forests with interspersed natural savannas in lowland Bolivia represents an excellent study system for advancing our understanding of the process of forest replacement by grass-dominated vegetation. The region known as Chiquitania contains a mosaic of vegetation types dominated by seasonally dry tropical deciduous forest interspersed with natural savannas that are western disjuncts of the Brazilian Cerrados (Killeen et al., 1990). The forests of Chiquitania are transitional between the more humid Amazonian forest to the north and the drier scrub woodlands to the south (Killeen et al., 2006). These forests are predicted to be particularly vulnerable to replacement by savanna due to seasonal drought and flammability (Hutyrá et al., 2005), and historic sensitivity to climate change (Mayle et al., 2000). These forests are also subject to the multitude of anthropogenic drivers of deforestation and forest degradation that operate throughout the Amazon Basin (Steininger et al., 2001). Importantly, the diverse native grass flora of Chiquitania, together with naturalized African forage grasses, permit investigation of the forest-replacing potential of a variety of grass species as well as the interaction between soils and grass species composition.

Soil fertility is thought to be a major determinant of natural savanna–forest distributions in South America (Hoffmann et al., 2009). In Chiquitania, natural savannas generally occur on shallow sandy soils or well-drained oxisols, whereas forests occur on younger, relatively fertile soils (Killeen et al., 1990). Given the huge range in soil characteristics that occur across the Amazon Basin (Quesada et al., 2009), a better understanding of associations between soil type and grass species assemblages is critical to move beyond simple assumptions that climate alone will determine vegetation shifts in the region.

We used satellite imagery to quantify the extent of forest replacement by grass-dominated vegetation between 1986 and 2005 in a 22,500 km² area of Chiquitania in lowland Bolivia. Based on this analysis, we identified and sampled natural savannas and newly de-

rived savannas (i.e., areas that changed from forest to grass-dominated vegetation between 1986 and 2005). We tested the hypothesis that derived savannas are floristically distinct from natural savannas based on grass and tree species compositions. We also tested whether native and derived savannas differ in fuel loads, fire histories, and soil characteristics. Information from this study could be used to improve deforestation models, to clarify the kinds of ecosystems that are likely to expand in response to global change, and to emphasize the conservation implications of different types of forest-replacing grassy vegetation (Bond and Parr, 2010).

2. Methods

2.1. Study area

This research was conducted in 22,500 km² of northern Chiquitania bounded by the limits of CBERS-2 satellite scenes and the San Ramon–Trinidad Highway on the southwest (Fig. 1). Primary towns in the region are Concepción (16°8'S 62°1'W; 500 m altitude; population 6900) and San Ignacio (16°22'S 60°57'W; 400 m altitude; population 24,000). The mean annual temperature in the region is 24 °C with extreme temperatures of 4–37 °C; mean annual precipitation is 1160 mm but ranges 799–1859 mm (data from *Administración de Aeropuertos y Servicios Auxiliares a la Navegación Aérea* collected in Concepción, 1943–2005). Seven months each year receive <100 mm precipitation (April through October) and during four months (June through September), potential evapotranspiration exceeds rainfall (Peña-Claros et al., in preparation).

2.2. Satellite image analysis

To quantify the extent of forest replacement by physiognomic savanna during 1986–2005, we digitally processed satellite images to create a change trajectory map that identified areas of forest transformed into grass-dominated vegetation. Due to the seasonality of the region and the predominance of deciduous trees, we chose images from the early to mid-dry season before complete leaf senescence but with many cloud-free days. For the 1986 classification, we



Fig. 1. Study location in eastern lowland Bolivia. The shaded area corresponds to the intersection of the Landsat TM (1986) and CBERS-2 (2005) satellite images analyzed to detect forest replacement by grass-dominated vegetation.

used adjacent 1986 Landsat Thematic Mapper (TM) scenes for Path 230 Row 071 and Path 229 Row 071 from 2 July 1986 and 27 July 1986, respectively, available from the Global Land Cover Facility, University of Maryland, USA. The Path 230 Row 071 scene was already orthorectified and we obtained an orthorectified scene for TM Path 229 Row 071 from 16 July 1988. Due to Landsat 7 technical failures and limited availability of more recent Landsat TM scenes, we chose two CBERS-2 (China–Brazil Earth Resource Satellite) scenes from INPE (National Institute of Space Research, Brazil) for Path 172 Row 118 from 24 July 2005 and Path 171 Row 118 from 27 July 2005. The data were projected to WGS84, UTM Zone 20 S, resampled to 30 × 30 m spatial resolution, and geo-referenced via image-to-image rectification using the orthorectified TM images with a root mean square (RMS) error of <0.5 pixels.

During June–July 2007, we visited 190 sites distributed across the study region to create the database of Geographic Positioning System (GPS) coordinates and corresponding vegetation descriptions needed to interpret current and historic satellite images. At each 30 × 30 m site (i.e., the size of one Landsat pixel), we measured tree canopy cover at three random points with a spherical densitometer held at 1.5 m (Lemmon, 1956) and visually estimated the percent ground cover of graminoids of any height. We also took digital photographs of each site and made notes on current and past land-use practices. For classification of the current image (Table 1), we defined each site as forest (≥65% tree canopy cover), savanna (>25% graminoid cover and <65% tree canopy cover, including grass and herb-dominated swidden fallows), agriculture (planted pastures and row crops), or wetland (any seasonally inundated area). A point was only assigned to different classes in 1986 and 2005 if there was convincing evidence that a shift had occurred.

We used a random selection of half of the training samples to create spectral signatures based on histogram-equalized CBERS-2 Bands 2–4 and histogram-equalized TM Bands 2–5 and then assigned pixels to the four classes using the maximum-likelihood model in Erdas Imagine 9.0. (Leica Geosystems, Norcross, Georgia, USA). Agriculture was largely, though not completely, separable from savannas based on spectral signatures alone, but because ranchers usually clear forests in a manner that creates regularly shaped borders (Steininger et al., 2001; Martínez et al., 2003), we were able to manually edit misclassified pixels as agricultural land. Manual editing could not correct all small planted pastures with irregularly shaped borders, but we account for this in the accuracy assessment and error corrections described below. Furthermore, we find this error acceptable because small or irregularly shaped patches of grass could represent an as yet undescribed form of derived savanna.

Once each of the images was classified, we used the remaining half of the training samples to perform accuracy assessments. The accuracy results we report are mean values for the two TM 1986

scenes and the two CBERS 2005 scenes weighted by their proportional contribution to the 1986–2005 change trajectory analysis. We used image subtraction to detect changes in pixel classifications between 1986 and 2005 to indicate areas where derived savanna replaced forest. Prior to overlaying classified images to produce the change trajectory map we created a mosaic of the two adjacent scenes for each year. We used the error matrix produced by the accuracy assessment to correct the total area estimates for each cover class and each trajectory class (van Deusen, 1996); both raw (map values) and corrected (unbiased) values for cover classifications are presented.

2.3. Savanna floristics, fuels, and soils

During the mid to late rainy season of 2008 (February–May), we conducted detailed field sampling of areas determined by satellite image analysis to have shifted from forest to savanna between 1986 and 2005. We used a stratified random sample of pixels from across the study region to identify grassy patches >9 ha that included 20 derived savannas and 12 natural savannas (i.e., areas classified as savanna in both 1986 and 2005). We excluded some grass-dominated sites (~10% of all derived savannas) in roadless portions of the study region.

In each selected site, we established five 20-m transects at random locations. Along each transect, we measured ground cover density and height up to 2 m at 41 points spaced at 0.5 m intervals of the following classes: (1) grass cover by species; (2) other herbaceous plants; (3) shrubs; (4) leaf litter; and, (5) bare soil. We also measured cover of grasses >2 m tall on these transects. To measure small diameter fuel loads, we clipped all standing biomass <25 mm stem diameter from 0.5 × 0.5 m plots at the ends and midpoint of each transect and separated the material into the following classes: (1) graminoids (i.e., Poaceae, Cyperaceae, Juncaceae); (2) other herbs; and, (3) shrubs. We also collected litter from these three plots (0.75 m²/transect) and sorted the material collected into graminoid litter or litter from all other sources. Species present in these plots but not at the 41 ground cover density points were assigned a cover value of 1%. To obtain more accurate estimates of standing biomass of the native bamboo *Guadua paniculata*, three 1 m² plots were destructively sampled by clipping all culms at ground level. After weighing biomass in the field, subsamples were dried at 65 °C for 48 h to correct for moisture content. At the ends and midpoint of each transect, we estimated tree canopy cover with a spherical densitometer held at 1.5 m. We identified to species and measured the DBH and height of all trees >5 cm DBH within 4 m of the transect (i.e., 20 × 8 m). To estimate the number of years since the most recent fires at each site, we inspected burnt and resprouted trees, checked for charcoal, and discussed our estimates with local land managers. As an indication of the intensity of past fires, we measured the maximum char height on the trunks of burned trees (Fry, 2008).

At the midpoints of each of the five transects at each site, we measured soil depth to 2 m with a bucket auger, collected soil samples for bulk density determination (0–4 cm) in 6.8 cm diameter tins, and extracted soil cores (0–20 cm, 6.8 cm diameter) for laboratory analysis. When soil was <20 cm deep, we collected an equivalent volume of soil from multiple shallow cores. We mixed the soil cores from each site before sending samples for analysis by the Center for Tropical Agriculture Research (CIAT) in Santa Cruz. Soils were analyzed for the following: pH (1:5 in water); electrical conductivity (1:5 in water); soluble cations – Ca, Mg, Na and K (atomic absorption following soil digestion in ammonium acetate but for Ca and Mg, soil was additionally treated with lanthanum chloride); interchangeable acidity (titration with potassium hydroxide of soil diluted in potassium chloride); Al (fluoride titration); available P (modified Olsen method for pH < 5.4, modified

Table 1

Tree crown and graminoid cover of training samples used for the satellite image classification, and natural and derived savannas included in the floristic study. Values are mean percents ±1SD.

	<i>n</i>	Tree canopy cover (%)	Graminoid cover (%)
<i>Training sample classes</i>			
Forests	81	89 ± 10	6 ± 12
Savannas	63	18 ± 18	79 ± 16
Agriculture	34	4 ± 6	85 ± 18
Wetlands/ water	12	–	–
<i>Floristic study sites</i>			
Natural savannas	12	22 ± 14	51 ± 16
Derived savannas	17	30 ± 19	50 ± 23

Bray and Kurtz method for $\text{pH} > 5.4$); total N (Micro-Kjeldahl method); organic matter (Walkley–Black method); and, texture (sedimentation analysis). Cation exchange capacity was calculated as the sum of interchangeable acidity plus the concentration of soluble cations (Ca, Mg, Na and K). Bulk density samples were oven dried at 105 °C for 24 h prior to weighing.

We identified grass species using the nomenclature of Renvoize (1998) with assistance of keys provided therein and by Killeen (1990). Nomenclature departs from Renvoize (1998) for the former *Brachiaria brizantha*, *Brachiaria decumbens*, and *Panicum maximum* that molecular data place within *Urochloa* (Aliscioni et al., 2003). Tree nomenclature follows Jardim et al. (2003) and Killeen et al. (1993). Identifications were confirmed at the Noel Kempff Mercado Museum of Natural History Herbarium in Santa Cruz, Bolivia (SCZ) where voucher specimens were deposited. Note that after first mention, species are referred to by their generic name (except where ambiguous).

2.4. Data analysis

Field sampling revealed that three of the 20 areas classified as derived savannas by satellite analysis were not savannas in terms of tree canopy cover and herbaceous ground cover. After excluding these wooded areas, we analyzed data from $n = 12$ natural savannas and $n = 17$ derived savannas. We used detrended correspondence analysis (DCA) to ordinate study sites based on their grass and tree species compositions. We performed two ordinations, one using percent grass cover by species and a second using tree basal area by species. Only species present in at least two sites were included; the grass and tree DCAs included 52 and 64 species, respectively. We performed both ordinations in R 2.9.0 (the R Foundation for Statistical Computing) using the *decorana* command from the *vegan* 1.15–2 package. To compare how grass and tree species belonging to particular vegetation associations (forests or savannas) or functional groups (native savanna grasses or exotic forage grasses) were distributed in natural versus derived savannas, we classified grasses and trees *a priori* based on species descriptions by Killeen (1990) and Jardim et al. (2003), respectively.

We compared natural and derived savanna diversity on the basis of numbers of species of native grasses, savanna trees, and forest trees; the proportions of all trees that were savanna species, forest species, or palms were also compared. To control for the effect of area sampled, we expressed species richness on a per transect basis. As such, values for each savanna are the average from five 20-m transects. The number of native grasses includes all species recorded in cover counts or present in three 0.5×0.5 m subplots per transect. The number of tree species (>5 cm DBH) were those present in each transect (160 m² sampled per transect). To compare numbers of species in natural and derived savannas we used Student's *t*-tests and Mann–Whitney U-tests. We used canonical correspondence analysis (CCA) to relate grass species composition to soil variables measured in natural and derived savannas. CCA was performed in R 2.9.0 using the *cca* command from the *vegan* 1.15–2 package. We tested for differences in soil characteristics between natural and derived savannas using *t*-tests. We compared natural and derived savannas on the basis of time since fire and char height on tree trunks, as well as total fine fuel loads and individual biomass components (i.e., graminoid litter, stand herbs, etc.) using *t*-tests and Mann–Whitney U-tests.

3. Results

3.1. Satellite image change analysis

The 1986 Landsat TM and 2005 CBERS-2 classifications had overall accuracies of 90% and 89%, respectively, with overall kappa

Table 2

Accuracy assessment of classified images used in the 1986–2005 change trajectory analysis.

Class	TM 1986		CBERS 2005	
	Producer's accuracy (%)	User's accuracy (%)	Producer's accuracy (%)	User's accuracy (%)
Forests	87	100	95	84
Savannas	96	76	78	91
Agriculture	83	100	92	97
Wetlands	100	86	83	100
Overall accuracy	90		89	
Overall kappa statistic	0.84		0.84	

values of 0.84 and 0.84 (Table 2). The 1986 and 2005 classifications differed in accuracy for forests and savannas (natural and derived) such that there was high confidence in pixels classified as forest in 1986 and high confidence in pixels classified as savanna in 2005 (Table 2). In the 1986 classification, user's accuracy (or consumer's risk, the probability that a classified pixel is indeed that cover class; van Deusen, 1996) for forests (100%) was greater than for savannas (76%), whereas in the 2005 classification user's accuracy for forests (84%) was less than savannas (91%). These values signify high confidence that areas classified as derived savanna in the change trajectory map (Fig. 2) were indeed formerly forest. The trade-off for confidence in detection of forest-replacing derived savanna is that the analysis provides a conservative estimate of savanna formation and overestimates succession from savanna to forest. After correcting for this trade-off, we estimate that between 1986 and 2005, total forest cover declined from 83% of the study area to 68%, savannas increased from 14% to 22%, and agriculture increased from 2% to 9%. Of the 17,700 km² classified as forest in 1986 in the change trajectory analysis, 4.5% (800 km²) changed to savanna by 2005 and 5.4% (959 km²) was converted to agriculture (Table 3); error-corrected values are 7.6% (1420 km²) and 6.4% (1200 km²), respectively. About 2000 km² was classified as savanna in both 1986 and 2005 and was defined as natural savanna for the floristic studies that follow.

3.2. Savanna floristics

Field sampling and subsequent DCA performed on grass species data showed two kinds of natural savannas: typical *cerrado* and areas dominated by *Guadua*. Natural savannas were clustered together on DCA axis-1 (Fig. 4a); 10 of 12 were floristically distinct from the derived savannas, a position in ordination space that corresponds with the DCA scores of native *cerrado* grasses (Fig. 3b and c). The two natural savannas that were not closely grouped with the *cerrados* contained the native bamboo *Guadua*, either as the dominant or mixed with *cerrado* grasses. Derived savannas were considerably more dispersed in ordination space than natural savannas (Fig. 3a). The positions of most derived savannas corresponded with the species scores of the following dominant grasses: *Guadua*, *Urochloa brizantha* and *Urochloa maxima*, *Imperata brasiliensis*, and *Digitaria insularis* (Fig. 3c). With the exception of a single derived savanna that had a grass flora similar to the *cerrados*, the only derived savannas that clustered near natural savannas were *Guadua*-dominated.

The tree DCA revealed a distinct cluster of natural savannas but little grouping of derived sites (Fig. 3d). The site scores for natural savannas corresponded to the species scores of *Curatella americana* (Dilleniaceae), *Qualea grandiflora* (Vochysiaceae), *Caryocar brasiliensis* (Caryocaraceae), *Diptychandra aurantiaca* (Caesalpinoideae), and other trees considered to be characteristic of savanna by Jardim et al. (2003; Fig. 3e and f). In contrast, the derived savannas

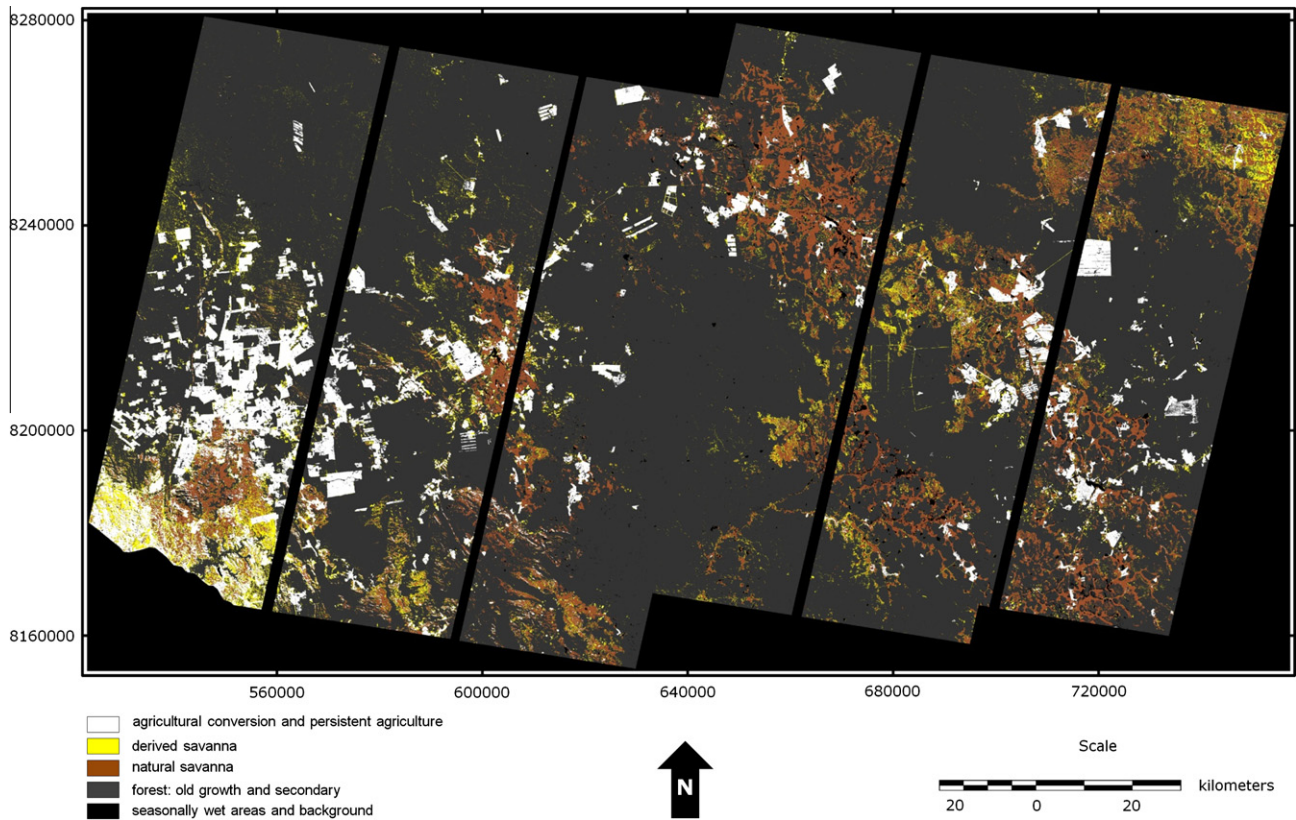


Fig. 2. Modified change trajectory map created from classified 1986 (Landsat TM) and 2005 (CBERS-2) images used to identify forest-replacing grass-dominated vegetation (derived savannas) and natural (old) savannas. Trajectory classes other than forest–savanna and savanna–savanna are grouped in the color coding for visual simplification; see Table 3 for clarification of color groupings. Axes are labeled with UTM coordinates for WGS 84 Zone 20 south. The four unclassified strips that transect the map correspond to pixels of low CBERS-2 image quality that were excluded from the analysis. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3

Area of change trajectory classes for 1986–2005. Map totals are the sums of all pixels (as indicated by the change trajectory analysis) that were used to identify natural and derived savannas for field sampling. Error-corrected estimates were adjusted based on the results of the accuracy assessment of the classified satellite images to more accurately reflect the area of each transition class.

Trajectory (1986–2005)	Trajectory class synonyms	Color Fig. 2	Map totals		Error-corrected estimates	
			km ²	(% of study area)	km ²	(% of study area)
Forest–forest	Forests	Gray	15,963	71.1	14,182	64.9
Forest–savanna	Derived savannas	Yellow	800	3.6	1418	6.5
Forest–agriculture	Agricultural conversion	White	959	4.3	1196	5.5
Savanna–forest	Forest succession	Gray	1713	7.6	1115	5.1
Savanna–savanna	Natural (old) savannas	Brown	1986	8.9	2579	11.8
Savanna–agriculture	Agricultural conversion	White	481	2.1	440	2.0
Agriculture–forest	Forest succession	Gray	42	0.2	62	0.3
Agriculture–savanna	Persistent agriculture	White	50	0.2	148	0.7
Agriculture–agriculture	Persistent agriculture	White	176	0.8	366	1.7
Water (in any year)		Black	268	1.2	340	1.6

typically contained a few remnant forest tree species such as *Anadenathera colubrina* (Mimosoideae; a dominant forest species), palms in the genus *Attalea* (*A. phalerata*, *A. speciosa*, *Arecaceae*), or species that occur across a range of habitats (e.g., *Astronium urundeuva*, *Anacardiaceae*). Whereas the grass ordination revealed two types of natural savannas (*cerrados* and those with *Guadua*), the analysis based on tree species composition showed all natural savannas as part of one distinct cluster. None of the derived savannas clustered amongst the natural savannas, but four sites had DCA-1 scores similar to natural savanna. These derived sites clearly differed from natural savannas along DCA-2 based on the presence

of *Anadenathera*, *Astronium*, *Attalea speciosa*, and *Magonia pubescens* (*Sapindaceae*).

Natural savannas supported more native grass species and greater numbers of savanna tree species than derived savannas, whereas derived savannas contained more forest tree species. The average numbers of native grass species per transect were 5.7 ± 0.6 and 1.7 ± 0.3 for natural and derived sites, respectively (mean \pm 1SE; *t*-test, $p < 0.001$). Median savanna tree species richness values per transect (160 m²) were 2.5 (range 1.2–5.8) and 0.4 (range 0–7.2) for natural and derived sites, respectively (Mann–Whitney U, $p < 0.001$). Mean forest tree species richness values per 160 m² were

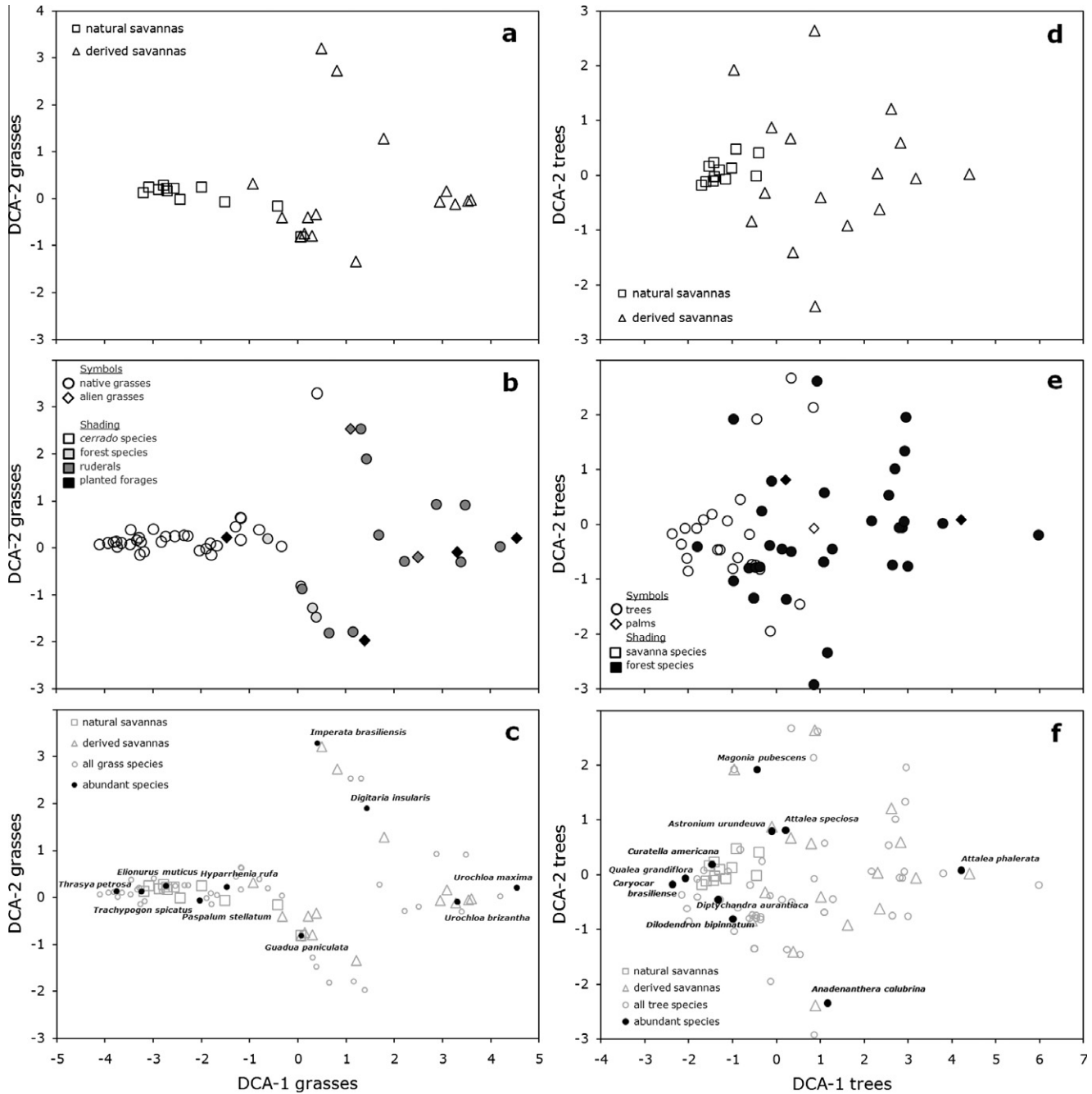


Fig. 3. Detrended correspondence analyses of natural savannas ($n = 12$) and derived savannas ($n = 17$) based on (a–c) grass cover by native and exotic species, and (d–f) tree species by basal area. Ordination plots display the scores for sites and species along the first two DCA axes. (a) Ordination of 52 grass species present in at least two sites. (b) Ordination of sites by grass species. (c) Composite ordination of sites and species with the ten most abundant grass species noted. (d) Ordination of sites by tree species. (e) Ordination of 64 tree species present in at least two sites; shading of species characteristic of savanna or forest is based on Jardim et al. (2003). (f) Composite ordination of species and sites with the ten most abundant tree species noted.

0.6 ± 0.1 and 1.3 ± 0.3 for natural and derived sites, respectively (mean \pm 1 SE; t -test, $p = 0.013$). The relative proportions of savanna trees, forest trees, and palms differed between natural and derived savannas with the former composed primarily of savanna tree species and the latter with a high proportion of forest trees. In natural savannas, 83% of trees were savanna species, compared to 22% in derived savannas (Fig. 4). Relative abundances of palms did not differ between savanna types, but they were most abundant in derived savannas. Finally, grass and tree species listed in order of their respective DCA-1 scores show the limited number of species shared by natural and derived savannas (Appendix A).

There were a few exceptions to the trend of high native grass diversity in natural savannas and low savanna tree diversity in derived savannas. One exception was a single derived savanna located in an area where forest and natural savanna are substantially intermixed. This savanna had the highest mean tree species richness of any site sampled (7.2 savanna and 4.4 forest tree species/transect) and was the only recently derived savanna that was similar to diverse natural savanna in grass and tree species composition. The exception to the relatively high grass species richness in natural savannas was a site where *Guadua* appeared to exclude most other grasses and that

contained few trees (only 1.4 savanna and 0.6 forest tree species per transect).

The majority of natural savannas sampled (11 of 12) and one of the newly derived savannas (1 of 17) contained a diversity of grass species typical of *cerrado* (Killeen et al., 1990; Killeen and Hinz, 1992). The most abundant species were the native grasses *Elionurus muticus*, *Trachypogon spicatus*, *Thrasya petrosa*, *Paspalum stellatum*, and the naturalized African forage grass *Hyparrhenia rufa*. In lower abundances but frequently present in *cerrado* were the native grasses *Andropogon selloanus*, *Axonopus barbigerus*, *Axonopus marginatus*, *Paspalum erianthum*, and *Schizachyrium sanguineum*. Of the 77 grass species encountered in this study, 36 occurred exclusively in *cerrados*.

Guadua was the dominant grass in 7 of 17 forest-replacing derived savannas. On the basis of their nearly arboreal habit, bam-

boos are commonly considered woody plants or are assigned a vegetation class of their own. In contrast, we consider bamboo-dominated areas with scattered trees to be savanna. *Guadua* produces large quantities of fine fuel and resprouts readily following fires (Veldman, 2008). *Guadua* stands, which dominate tens of thousands of hectares in the region (Killeen, 1990), can be characterized by frequent fires and severely charred or dead trees (Veldman, 2008). Although *Guadua* can grow up to 7 m tall, most stands reach only 2–5 m. Given its interactions with fire, it seems appropriate to include *Guadua* within the conceptual framework of grass-fire feedbacks influencing forest-to-savanna conversion.

Four exotic forage grasses of African origin were among the most common species encountered in this study. *Urochloa*-dominated areas (*U. brizantha*, *U. decumbens*, and/or *U. maxima* occurring alone or in mixed swards) accounted for six of 17 derived

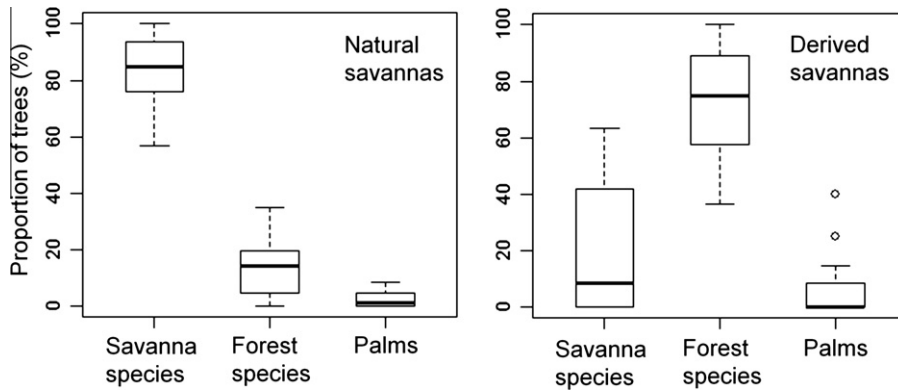


Fig. 4. Proportion of savanna tree species, forest tree species, and palms in natural savannas ($n = 12$) and derived savannas ($n = 17$). Natural and derived savannas differed in proportions (% of total stems >5 cm DBH) of savanna and forest species (t -tests, $p < 0.001$).

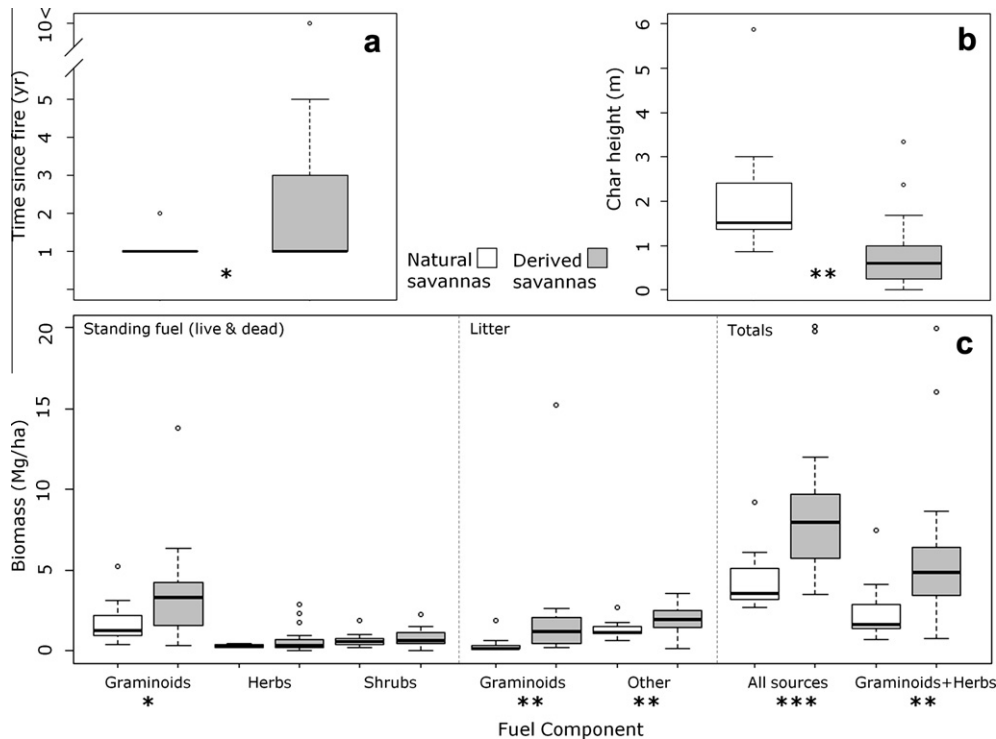


Fig. 5. Fire histories and fuel loads of natural ($n = 12$) and derived savannas ($n = 17$). (a) Number of years since the most recent fire. (b) Char heights on tree trunks. (c) Fuel loads produced by graminoids (Poaceae and Cyperaceae), herbs, and shrubs. Fuel loads are dry weights of biomass <25 mm diameter. Graminoid + herbs includes standing graminoid fuel, standing herb fuel, and graminoid litter. Asterisks (*) denote differences based on Mann–Whitney U and t -tests (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

savannas. Both *U. maxima* and *U. brizantha* are bunch grasses whereas *U. decumbens* spreads laterally via stolons. All three species form dense canopies, with *U. maxima* (2–3 m tall) typically exceeding the heights of *U. brizantha* and *U. decumbens* (1–1.5 m tall). Another widely naturalized African pasture grass, *Hyparrhenia*, is common in *cerrados* but rarely occurred in derived savannas. Two of the derived savannas that developed on abandoned swidden agriculture plots contained stands of *I. brasiliensis*. *Imperata* is a rhizomatous native grass that was a frequent component but never abundant in natural savannas. A third area of long-fallow swidden agriculture was dominated by the native annual herb *Hyptis suaveolens* (Lamiaceae). *Hyptis* formed a canopy of 1.5–2.5 m tall and appeared to exclude most other plants including grasses; the only trees interspersed with *Hyptis* were palms with charred trunks indicative of intense fires. *D. insularis*, a native ruderal, was abundant on a single site where it grew amongst burnt slash on the border of a pasture; *Digitaria* was also present in fallowed swidden plots dominated by *Imperata*.

3.3. Fuel loads and fire history

All natural savannas and 16 of 17 derived savannas showed signs of recent (within 5 years) fires, with median time since last fire of 1 year. But whereas all natural savannas had burned within 1 year, time since fire in derived savannas ranged 1–5 years (Fig. 5a). Maximum char heights in natural savannas (2.0 ± 1.4 m) exceeded those in derived savannas (0.8 ± 0.9 m; mean \pm 1SD; Fig. 5b). Compared to natural savannas, derived savannas had higher biomass of standing graminoids, graminoid litter, and other litter; there were no differences in herb or shrub biomass (Fig. 5c). Total fuel loads (biomass <25 mm diameter) in derived savannas (median 8.0 Mg/ha; range 3.5–20) were twice that of natural savannas (median 3.6 Mg/ha; range 2.7–9.2; Fig. 5c). Median fuel loads of standing graminoids, standing herbs, and graminoid litter (woody shrubs and other litter excluded) were 2.4 Mg/ha (range 0.7–7.5) and 6.2 Mg/ha (range 0.8–20) in natural and derived savannas, respectively (Fig. 5c). All natural savannas and 16 of 17 derived savannas contained charred trees.

Table 4
Soil variables measured in natural savannas ($n = 12$) and derived savannas ($n = 17$) listed in increasing order of CCA-1 axis scores relating grass species and soil variables. Asterisks (*) denote significance differences based on *t*-tests.

Soil variable	Natural savannas (mean \pm 1SD)	Derived savannas (mean \pm 1SD)	<i>p</i>	CCA-1
Bulk density (g/cm ²)	1.25 \pm 0.11	1.03 \pm 0.10	***	−0.84
Acidity (cmol/kg)	0.9 \pm 0.7	0.1 \pm 0.1	**	−0.69
Al (cmol/kg)	0.5 \pm 0.7	0.0 \pm 0.0	*	−0.61
Sand (%)	63 \pm 10	51 \pm 17	*	−0.40
Clay (%)	17 \pm 8	17 \pm 4	ns	0.00
Na (cmol/kg)	0.10 \pm 0.02	0.12 \pm 0.05	ns	0.12
Depth (m)	1.3 \pm 0.7	1.5 \pm 0.6	ns	0.26
P (mg/kg)	1 \pm 0	5 \pm 6	*	0.28
K (cmol/kg)	0.16 \pm 0.07	0.30 \pm 0.15	**	0.34
Silt (%)	21 \pm 11	31 \pm 16	*	0.39
pH	5.2 \pm 0.5	6.4 \pm 0.6	***	0.44
Electrical conductivity (μS/cm)	19 \pm 9	75 \pm 52	***	0.48
Cation exchange capacity (cmol/kg)	2.5 \pm 0.7	6.6 \pm 3.4	***	0.51
Ca (cmol/kg)	0.9 \pm 0.4	4.5 \pm 2.6	***	0.56
Mg (cmol/kg)	0.5 \pm 0.3	1.5 \pm 0.8	***	0.61
N (%)	0.09 \pm 0.04	0.17 \pm 0.05	***	0.64
Organic matter (%)	1.0 \pm 0.6	2.3 \pm 0.4	***	0.81

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

3.4. Soil fertility and grass species composition

Concentrations of plant essential nutrients (N, K, Ca, and Mg), cation exchange capacities, electrical conductivities, organic matter contents, pH, and silt were greater in derived than natural savannas (Table 4). Natural savanna soils were generally sandy, with high Al, acidity, and bulk density (Table 4). Natural and derived sites did not differ in clay content, Na concentration, or soil depth. A CCA of grasses and soils showed very similar clustering of sites and species compared to DCA of grass species only (Appendix A, Fig. 3 respectively). CCA-1 appears to represent a soil fertility gradient with most natural savannas (*cerrados*) occurring on infertile soils and derived savannas occurring on fertile soils (Appendix A).

4. Discussion

4.1. The grasses that replaced forests

Over a 20 year period (1986–2005) in eastern lowland Bolivia, satellite image analysis indicated that derived savanna replaced tropical dry forests at approximately the same rate as forest was cleared for agriculture. This new grass-dominated vegetation was floristically distinct from natural savannas and was dominated by a native bamboo, a few exotic forage grasses, or native invaders of fallowed swidden plots. Of the common species in forest-replacing derived savannas, high abundance of *Guadua*, *Urochloa* spp., *Imperata*, and *Hyptis* appears to be promoted by positive feedbacks with fire. Indeed, 16 of 17 derived savannas had burned within the previous 5 years.

The species common in derived savannas, or their congeners, are recognized for their fire-promoting characteristics, invasiveness, and dominance. Many bamboo species promote fire (Keeley and Bond, 1999) and bamboo stands are thought to be an alternative stable state to broadleaf forest in both temperate (e.g., *Arundinaria gigantea*; Gagnon and Platt, 2008) and Neotropical (e.g., *Guadua sarcocarpa* and *G. weberbauerii*; Griscom and Ashton, 2003, 2006) regions. *Imperata*, a native rhizomatous grass, is described by Killeen (1990) as “a serious pest in banana and coffee plantations” and Renvoize (1998) mentions *Imperata* stands as one type of anthropogenic savanna in lowland Bolivia. In northern Bolivia, *Imperata* abundance in small-scale agriculture plots was reported to increase with each slash-and-burn cycle (Sools, 2007); in Peru, *Imperata* invasion of swidden plots followed by repeated fires was considered critical step in the conversion of forest to savanna (Scott, 1977). An ecologically similar congener of Asian origin, *I. cylindrical*, has changed fire regimes and replaced natural vegetation in the southeastern United States (e.g., Lippincott, 2000); it is considered one of the most invasive plants in the world (MacDonald, 2004). *Hyptis*, a native Neotropical herb, is invasive in India where it colonizes shifting agriculture sites and reportedly enhances dry-season fires (Murthy et al., 2007). Additionally, *Hyptis* reputedly limits the germination and growth of both grasses and trees through alleopathy (Totey et al., 1994; Mokot et al., 2005).

Pasture grasses in the genus *Urochloa*, introduced from Africa as cattle forages, are now widespread in the Neotropics (Parsons, 1972). In eastern lowland Bolivia, *U. brizantha* and *U. maxima* are the most common planted pasture species, occur abundantly as roadside weeds, and invade disturbed forests in areas that are traversed by seed dispersing motor-vehicles (Veldman and Putz, 2010). Because these forage grasses are both intentionally planted and accidentally introduced (Veldman et al., 2009), it is difficult to ascertain the genesis of all *Urochloa* stands in this study. If we were to assume that all six *Urochloa*-dominated sites represent intentional planted pasture expansion, our estimate of agricultural conversion (Table 3) would increase from 5.5% to 7.1%

of the study area; the remaining derived savannas would still represent 920 km² (4.2% of the study area) where grass and herb-dominated vegetation, but certainly not planted pasture, replaced forest.

4.2. Soil fertility, species composition, and fuel loads

Soil fertility helps explain differences in grass species composition between natural and derived savannas (Table 4; Appendix A). Consistent with previous studies in the region (Killeen et al., 1990; Killeen and Hinz, 1992), we found natural savannas predominantly on nutrient-poor acidic soils. In contrast, derived savannas occurred on relatively fertile soils normally associated with forests – not surprising for sites that were forests within the last two decades. The absence of native savanna grasses in most forest-replacing savannas may be due to propagule limitation, a competitive disadvantage on fertile soils, or both. Native savanna grasses adapted to infertile soils are probably unable to take advantage of nutrients available in more fertile sites. In contrast, grasses with high potential growth rates (e.g., *Guadua* and *Urochloa* spp.) are physiologically ill-equipped for infertile soils, but are able to exploit disturbed forest soils that tend to be richer in nutrients (Grime et al., 1997). An apparent consequence of productive grasses and broadleaved herbs growing on fertile soils is that fuel loads in derived savannas were twice those of natural savannas. Interestingly, we found no relationship between time since fire and standing fuel loads, which suggests that the larger fuel loads in derived savannas are not simply due to longer fire return intervals compared to natural savannas.

4.3. Human land-uses and vegetation shifts

Superimposed on vegetation and underlying soil characteristics are human land-uses. As such, we should expect the determinants of derived savanna expansion to be more complicated than simply being driven by soil fertility and fire history, the factors that typically define natural savanna–forest boundaries (Hoffmann et al., 2009). When people clear forests for agriculture they prefer the most fertile soils, and when they establish pastures they intentionally introduce exotic forage species. People also manage cattle, which are nearly ubiquitous in Chiquitania. All of the natural savannas and 13 of 17 derived savannas contained at least one cattle trail, and densities of cattle dung piles were $42 \pm 50 \text{ ha}^{-1}$ and $57 \pm 76 \text{ ha}^{-1}$ for natural and derived savannas, respectively (mean \pm SD; Veldman, unpublished data). Cattle are clearly the dominant large herbivores in both natural and derived savannas, and certainly influence plant community assembly, fuel loads, and seed dispersal in ways that warrant further study.

Forest replacement by species-poor derived savanna is just one sort of vegetation shift in lowland Bolivia. Although this study focused on places transformed from forest to grass-dominated vegetation, selective logging, fires, and swidden agriculture can result in a variety of vegetation states (Pinard et al., 1999; Putz and Redford, 2010). Although our data support other reports that swidden fallows are invaded by fire-promoting grasses and herbs (Scott, 1977; Killeen, 1990; Renvoize, 1998; Sools, 2007), the sorts of derived savannas we found are not the only fate of abandoned agricultural land. Indeed, the remote sensing analysis showed 10% of the area classified as agriculture in 1986 had regenerated to forest by 2005.

4.4. Implications for “savanna” expansion in the Amazon Basin

The use of climate data from South American’s natural savannas to predict savanna expansion through the Amazon Basin (e.g.,

Malhi et al., 2009) may be misleading because derived savanna species are not functional equivalents of the species found in old-growth natural savannas (e.g., derived savannas had larger fuel loads and some of the invading grass species are not C₄). Additionally, underlying environmental gradients (i.e., soil fertility) and human-activities (e.g., logging, swidden agriculture) favor a few grass species over many native savanna species. Natural savannas may expand in areas with low soil fertility, but when grass populations expand onto fertile forest soils, they are typically composed of just a few species that produce large fuel loads. These differences in fuel loads are relevant because of differences in fire-tolerance between tree species characteristic of forest compared to natural savanna (Hoffmann et al., 2009); in lowland Bolivia and throughout much of the Amazon Basin, forest trees are susceptible to even low-intensity fires (Pinard and Huffman, 1997). Given that most of the trees we found in derived savannas were forest species unlikely to survive repeated grass-fueled fires, maintenance of tree cover may depend on whether savanna tree species are able to colonize. Conversely, in the absence of fire, the presence of forest tree species may facilitate forest regeneration.

This study was conducted in a region that contains natural savannas, but in forests that are far from natural savannas, the likelihood of natural savanna expansion seems even less likely, at least over decadal or centennial time scales. Although it is clear that repeated fires can push forests into a severely degraded state (e.g., Barlow and Peres, 2008), the presence of one or more forest-invading and fire-promoting grasses may be a trigger that promotes forest-to-savanna conversion (Cochrane et al., 1999). Data collected in forests that are currently far from propagule sources of invasive grass species may be quite different than those subjected to the synergistic effect of disturbance and forest-invading grasses. Clearly more needs to be learned about the biology of the grasses, herbs, and trees that dominate recently derived savannas as compared to those characteristic of natural savannas. Species differences in fine fuel production, photosynthetic pathways, heights, soil nutrient requirements, seed production, capacity for vegetative expansion, and drought resistance could result very different vegetation-climate-fire interactions in tropical regions.

5. Conclusions

The grass-dominated vegetation that replaced tropical forest in this study had low native species diversity, was floristically distinct from natural savannas, was usually dominated by one or two grass species, and contained remnant forest tree species. The distinction between diverse natural savannas and low-diversity derived savannas is important given the threatened status of the natural savannas of South America and predictions that Amazonian forests are increasingly susceptible to savanna expansion. Soil fertility should be considered when predicting which grass species are likely to replace forests; fertile soils are more likely to be colonized by a few highly productive native or exotic species rather than native savanna grasses. Species identities are important because grass species with high growth rates produce large fuel loads on fertile soils, and thin-barked forest tree species are less fire tolerant than thick-barked savanna species. The large difference in species richness and floristic composition between natural savannas and newly derived savannas in this study underscores the contrasting biodiversity implications of natural savanna expansion compared to forest replacement by other kinds of grass-dominated vegetation. As research on large-scale tropical forest–savanna dynamics progresses, we ought to be explicit about what kind of “savanna” is involved.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.01.011.

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