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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 km^2 of eastern lowland Bolivia. Analysis of Landsat TM and CBERS-2 satellite imagery revealed that, in addition to 1200 km^2 (7.1%) of deforestation for agriculture and planted pastures, 1420 km^2 (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.

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., Hutyra 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 (Hutyra 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 km^2 area of Chiquitania in lowland Bolivia. Based on this analysis, we identified and sampled natural savannas and newly derived 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 km^2 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.