Biodiversity and Conservation
https://doi.org/10.1007/s10531-019-01720-z

ORIGINAL PAPER

Redefining the Cerrado–Amazonia transition: implications for conservation

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Received: 3 May 2018 / Revised: 19 November 2018 / Accepted: 14 February 2019

Abstract
Understanding the nature and extent of ecosystem boundaries has important implications for the management and conservation of biodiversity. However, characterizing and establishing such boundary limits has been a persistent challenge worldwide. The Cerrado–Amazonia transition (CAT) in Brazil is the world's largest savanna-forest transition. However, the CAT is represented in official maps used by Brazilian governmental agencies as a simple line separating the two biomes. Here, we demonstrate that the CAT is in fact broad, complex and interdigitating and that its traditional linear representation is not adequate for recognizing and conserving biodiversity in this region. Over the 30 years of our analysis, the CAT suffered more deforestation than the forests and savannas in each individual biomes (Amazonia and Cerrado). The complexity of tropical savanna-forest boundaries has been misunderstood and misrepresented by current maps, severely threatening the complex CAT biota. As a consequence, vegetation losses have reached levels close to collapse in areas of intense human activity.

Keywords Ecotonal forests · Official mapping · Arc of deforestation · Biodiversity losses · Land use · Deforestation · Ecosystem boundaries

Communicated by Guarino Rinaldi Colli.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10531-019-01720-z) contains supplementary material, which is available to authorized users.

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Introduction

Tropical ecotones between large biomes require more complex, deeper studies for biodiversity conservation measures due to the environmental complexity and species exchange from one biotic community to another. Such an intricate ecological condition is typical in large-scale contact areas, such as the Cerrado/Amazonia transition (CAT), the world's largest tropical ecotone (Torello-Raventos et al. 2013). The vegetation across the CAT not only represents a mix of species but also a unique model to investigate tropical biodiversity and savanna-forest dynamics (Marimon et al. 2014) in the context of ecosystem functioning, carbon and nutrient cycles (Oliveira et al. 2017; Peixoto et al. 2017). Moreover, the forests in these regions may be the first to suffer the combined effects of tree species loss by climate changes (Esquivel-Muelbert et al. 2018) and deforestation. Similarly, cerrado vegetation in this region has experienced the effects of accelerated deforestation. Therefore, defining savanna-forest limits and understanding their spatial–temporal dynamics are crucial for biodiversity conservation planning and management.

As a large-scale area that exceeds 6,000 km in length, the CAT is by far the largest savanna-forest transition on the planet, separating the Cerrado—the greatest and most diverse savanna—from Amazonia—the most extensive tropical forest worldwide. Previously recognized as an ecological tension zone (Brasil 1981), the CAT is characterized by a highly seasonal climate, nutrient-carbon hypercycling (Oliveira et al. 2017; Valadão et al. 2016) and vegetation hyperdynamics, i.e., the tendency to have much faster stem recruitment and mortality rates than in the core areas of Amazon (Marimon et al. 2014; Phillips et al. 1998). The hyperdynamic vegetation can be more vulnerable to environmental changes because such condition indicates disequilibrium in the balance of biomass and nutrients (Oliveira et al. 2017; Marimon et al. 2014). Therefore, the ecosystems of CAT can also respond faster in terms of functioning (e.g. hyper nutrient cycling and biomass flux) to environmental changes in relation to core areas of Amazonia and the Cerrado. The CAT is also an agricultural frontier, known as the "Arc of Deforestation" (Nogueira et al. 2007, 2008), owing to its rapid and continuous conversion of natural areas into agricultural systems and pastures (Marimon et al. 2001; Alencar et al. 2004; Fearnside 2005) and to selective timber logging and forest fires (Matricardi et al. 2010, 2013). These environmental conditions contribute to the intricate and dynamic features of the CAT, hampering its precise delimitation in both space and time. This is one of the main causes of the current complexity of the CAT in relation to biodiversity conservation.

Therefore, accurate mapping can be used as a key tool for planning public policies for biodiversity conservation, environmental zoning and land use management in large-scale. However, previous mapping efforts led by the RADAMBRASIL Project of Brazilian Institute of Geography and Statistics (IBGE), the official institution for mapping in Brazil, represented the CAT as a simple line. The RADAMBRASIL Project used radar images and extensive fieldwork between 1970 and 1985 to define the limits between Brazilian biomes, and these limits are still currently in use. However, the delimitation by this former official mapping project in Brazil based on radar images was not precise to yield an accurate spectral discrimination of vegetation types. Despite the excellence of such surveys, radar-based methodology, originally developed for geological purposes, is flawed for vegetation and biodiversity mapping, especially when accounting for the wide, complex and interdigitating nature of the CAT. Therefore, it is not adequate for understanding biogeographical distribution patterns in such complex areas or for conservation planning and management in the agricultural frontier in Brazil.

The complexity of the CAT was first reported by Soares (1953) and Ducke and Black (1953), who defined the meridional and oriental limits of the Amazon Forest. Recent studies have confirmed this pattern but have also questioned the conventional Cerrado–Amazonia limit by revealing a floristically complex transition zone (Marimon et al. 2006; Ivanauskas et al. 2008; Mews et al. 2012). For example, ombrophyllous forest, seasonal forest, Cerradão (ecotonal forest) and Cerrado savanna formations are in frequent contact in this region (Ratter 1993; Ivanauskas et al. 2008), characterizing an especially difficult condition for mapping and recognizing its boundaries. The CAT is also dynamic throughout short geological time periods, due to forest and savanna expansion and retraction events (Ab'Saber 2002; Pessenda et al. 2010; Ronnenberg 2013), and recent historical time periods—for instance, a 7-km encroachment of forest into savanna occurred in eastern Mato Grosso State between 1960 and 2000 (Marimon et al. 2006). These characteristics made it difficult to draw up highly detailed mapping of the CAT to guide the development of more effective public policies on nature conservation (e.g. planning based on more realistic maps of vegetation). Meanwhile, extensive habitat conversion by deforestation and burning has been a common practice in CAT. For example, Alencar et al. (2004) estimated that forests originally covered 362,500 km^2 (41%) of Mato Grosso state, an area equivalent to all of Germany. These forests lost 62% of their original cover to cattle farming, agriculture, timber logging, hydroelectric power and sugarcane ethanol production (see Brando et al. 2013).

In such unfavorable scenarios, the issue of Brazilian Forest Code and traditional mapping still prevail, which the border establishes that a simple, often arbitrary line separates Amazonia from the Cerrado and protect only 35% of vegetation considered as savanna but 80% of forests (Papp 2012). Moreover, the highly seasonal climate, typical of the CAT, boosts dry season fires that equally threaten both savanna and forest ecosystems (Alencar et al. 2004; Silvério et al. 2013; Matricardi et al. 2013). Consequently, habitat conversion and fires disturb and fragment continuous stretches of natural vegetation, transforming the CAT into a mosaic of scattered, poorly connected vegetation fragments. This prevailing scenario of the CAT is concerning due to the extensive loss of ecosystem function and biodiversity.

Herein, we use satellite imagery to map a large, representative central area of the CAT (613 km^2) to address four questions: (1) Could the CAT be better represented by a complex, varying and meandrous zone rather than the widely used simple division line? (2) Which area size and width best define the CAT? (3) Which type of native vegetation in the CAT is more affected by habitat conversion? (4) What are the implications of inadequate CAT mapping for biodiversity conservation? We demonstrate that the CAT consists of a much larger and complex area than previously represented in official maps and that the conversion of native vegetation has resulted in greater loss of unique habitats than in either Cerrado savannas or Amazonian forests.

Materials and methods

Study area

The study area comprised a large zone delimited by a 200-km buffer around the traditional line dividing the Cerrado and Amazonia according to the IGBE (2004), amounting to 8° of latitude and 12° of longitude in the Brazilian states of Mato Grosso, Pará, Tocantins and

Goiás (Fig. 1). This area was delimited based on the locations of 57 permanent plots established for field vegetation surveys conducted since 1996 by the Plant Ecology Laboratory, Universidade do Estado do Mato Grosso, Nova Xavantina Campus (Marimon et al. 2014). The points were identified by the main types of vegetation in the CAT, such as savannas, dense forests and more open transitional forests (e.g., *cerradão*).

To classify vegetation and land use types in the study area, we utilized Landsat-5 TM satellite images for 1984 (low land-use impact) and 2014 (high land use impact), with 30-m pixel spatial resolution, covering 900 m^2 per pixel in bands 1–5 and 7. Images were obtained from the Instituto Nacional de Pesquisas Espaciais–INPE (Brazilian Space Agency) (http://www.inpe.br/), originally from a UTM Projection System, Datum WGS-84. All Landsat scenes used were checked and adjusted to a cartographic base of rivers, roads and highways, provided by the IBGE (2014). Afterwards, images were converted to the Albers Conic Projection System, Datum SAD69.

Radiometric correction of images

We conducted a radiometric correction for image refinement, eliminating noise caused by atmospheric gases and particles in suspension. This process is necessary to normalize events diminishing the capture quality of the satellite sensor, such as variation in distance, incidence and angle of the Sun in relation to Earth (Matricardi et al. 2010), as well as displacements caused by variations in the platform of the sensor capturing the scene. This correction involves the conversion of the digital number in radiance and, subsequently, in

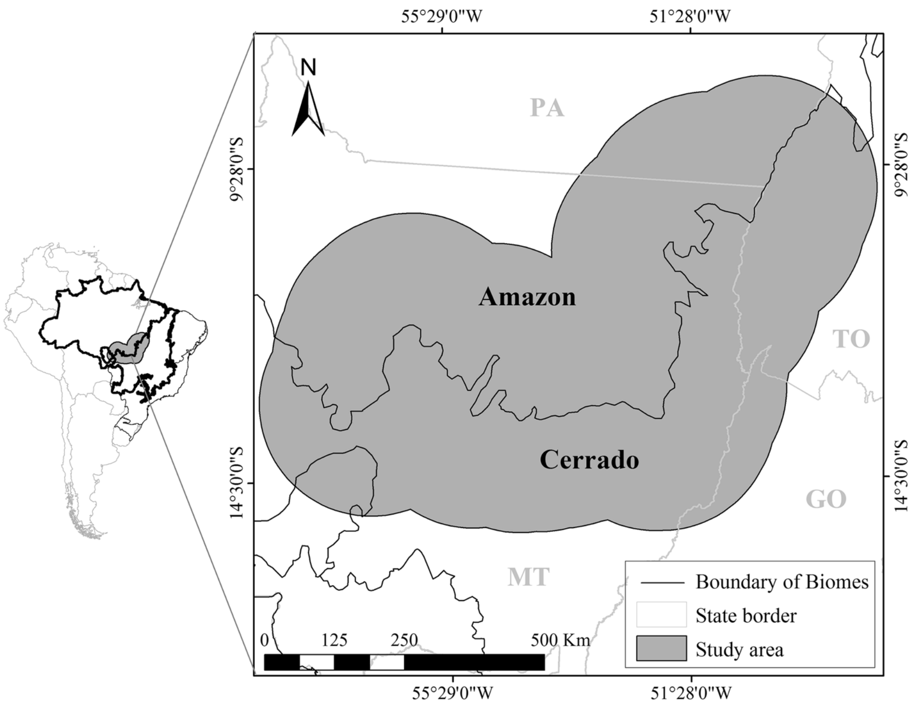

Fig. 1 Study area location in the Cerrado–Amazonia transition in Brazil

reflectance (Matricardi et al. 2013). Each scene used has a different characteristic for calibration. To address this condition, we used ERDAS (2011) and followed the calibration coefficient data available from the image metadata.

Spectral mixture analysis (SMA)

The fraction images derived from spectral mixture analysis (SMA) served as the input for supervised image classification. SMA fraction images were generated by identifying pure pixels of each component using ENVI 4.1 (ENVI 2004). Adams et al. (1995) indicated that the spatial mixture proportions (class or abundance fractions) of each reflectance pixel data from the Landsat TM satellite can be estimated by SMA, changing from pixel to pixel. SMA assumes that spectral signatures or endmembers (pure spectra) are physical endmembers showing maximum abundance in the scene containing the image (Meneses and Almeida 2012). In our analysis, we estimated four endmembers: soil, shade, green vegetation and non-photosynthesizing (dead or dry) vegetation derived from SMA, based on surface material classes and in six bands (1–5 and 7) of the Landsat-5 TM images. To resolve the SMA model, we used the selected endmembers, identified by applying the PPI (pixel purity index) technique available in ENVI as suggested by Matricardi et al. (2013). Lastly, we used the SMA model to classify the different land uses and land covers in the CAT as well as to produce the final mapping.

Image classification

An automatic supervised classification was used to generate a raster file of five land cover classes: (1) dense forest, (2) ecotonal forest, (3) savanna, (4) anthropic use and (5) water bodies (5). The dense forest class (1) comprises seasonal forests, ombrophyllous forests and ombrophyllous mixed forests. Ecotonal forest class (2) comprises phytophysiognomies of cerradão (the augmentative of Cerrado in Portuguese) dystrophic facies and sand soil carrasco (sensu Ratter et al. 1973). Cerradão vegetation, according to Ratter et al. (1973), is a connection between the Amazonian transitional Dry forest and the Brazilian savanna Cerrado, which may have a width that often reaches 4 km. This ecotonal vegetation was also described in terms of other particularities, as biomass hyperdynamic (Marimon et al. 2014), higher biomass than the cerradões of the core area of the Cerrado Biome (Morandi et al. 2018) and successional condition of advance over cerrado areas (Marimon et al. 2006; Morandi et al. 2016a; Passos et al. 2018). These contact forests of cerradão were also described by RADAMBRASIL Project (Brasil 1981) as another condition of ecological tension area with cerrado vegetation (tension of savanna vs. forest). The savanna class (3) includes savanna phytophysiognomies of dense, typical, sparse and outcrop rocky Cerrado, as well as cerrado of paleodunes, grasslands and seasonal flooding vegetation of "murundus fields", "veredas" and "palmeiral", all belonging to Cerrado Biome, as described by Ribeiro and Walter (2008). The anthropic use class (4) represents deforestation and all other land use change processes, as crops and pastures. Lastly, water class (5) includes water bodies of rivers, streams and lakes, among other.

The signature editor tool in ERDAS (2011) was used for that classification. Subsequently, a majority filter was applied to remove isolated pixels, noises in the image representing a classification error. We then recodified all the images to build the classification mosaic. Afterwards, we manually reconditioned and reclassified a few areas. To confirm and reclassify those areas, we used the permanent forest plots data of the

Plant Ecology Laboratory, Universidade do Estado do Mato Grosso, Nova Xavantina Campus (Marimon et al. 2014).

Delimitation of the ecotonal forest band

We generated a filter from the classified image to determine the transition area. We were able to resample using a 5-km^2 grid size over the classification using the following rules we determined for the present work based on ERDAS tool (Erdas 2011):

$$\mathrm{CL} = 1 \text{ if } adf \geq 50\%$$

$$\mathrm{CL} = 1 \text{ if } as \geq 50\%$$

$$\mathrm{CL} = 1 \text{ if } aef \geq 50\%$$

$$\mathrm{CL} = 1 \text{ if } aau \geq 50\%$$

$$\mathrm{CL} = 1 \text{if } anc\,(anc = aef) \geq 50\%$$

In this equation, CL is the cell class, *adf* is the percentage of dense forest cover, *as* is the percentage of savanna cover, *aef* is the percentage of ecotonal forest cover, *aau* is the percentage of anthropic use cover, and *anc* is the percentage where none of those classes dominated (Appendix Fig. A1). CL = 1 represents a set of pixels within a grid. The filter result was used to extract the ecotonal (transitional) forest from which we excluded patches smaller than 50 km^2 to reduce error. After transforming the image into vector format, we applied a smoothing tool using ArcGIS 10.1 (ESRI 2011) and some manual adjustments to clear the image from abrupt angles (Appendix Fig. A2). Using the end result of the smoothing tool and a fixed scale of 1:500,000, we manually generated another vector file to correct for areas not detailed by the filter and, using a fine adjustment, to connect areas not connected by the filter. The scale used in this work is appropriated to achieve the desired results in a timely and accurate manner to describe the boundaries of vegetation.

Deforestation analysis

We used deforestation vector files gathering data since 2014 for the entire Legal Amazonia from the Amazon Deforestation Monitoring Project–PRODES, provided by INPE. We also used files for 2010 from the Projeto de Conservação e Utilização Sustentável da Diversidade Biológica Brasileira–PROBIO (http://www.mma.gov.br/biodiversidade/projetos-sobre-a-biodiveridade/item/486). These files show vegetation cover and land use data for the Cerrado. Using ArcGIS 10.1, we selected only PROBIO's deforestation and anthropization classes. Next, we combined vectors using the dissolve tool, generating a single file comprising the entire area (Congalton 1997). We then transformed the vector file into a raster file using the polygon-to-raster conversion tool in ArcGIS 10.1 (ESRI 2011). To quantify deforestation and vegetation loss, we superimposed this image over the classification mosaic of the study area and performed an automatic count of pixels related to deforestation using the attributes table. Because the area of each pixel is known (900 m^2), we converted the resulting pixel counts to km^2.

Results

Our results reveal a transition band throughout the study site, with large variation in width (~40–250 km), as well as a complex mosaic of savanna and forest vegetation patches, with intrusions of both savanna in the forest matrix and forest in the savanna matrix. The mosaic was composed by 719 patches of forest (> 5 km^2) within the Cerrado Biome and 151 patches of Cerrado sensu stricto (> 5 km^2) within the Amazonia Biome (Fig. 2). Such results reveal that the CAT is not homogeneous and does not enable us to clearly define the limits between the Cerrado and Amazonia. In contrast, forests and savannas alternate in the landscape without precise width, limit or equal distribution. In many locations, forest intrusions follow lowland areas in the *Rio das Mortes* and *Rio Araguaia* river valleys from the start of the Bananal Sedimentary Plain (sensu Brasil 1981) to the south until its northernmost point.

Our final map shows a complex ecotone of 152,180 km^2 with 16 polygons ranging from 151 km^2 to 107,270 km^2 (Fig. 3), forming a much larger band than traditionally reported in the literature and official maps (e.g., Brasil 1981; IBGE 2004).

The superimposition of the IBGE line over our map indicates that nearly half of the ecotonal forest (7655 km^2) is within the Cerrado limits. The original line defined by the IBGE (2615 km throughout our study area) is nearly three times smaller than that estimated in this study (6420 km) (Appendix Fig. A3).

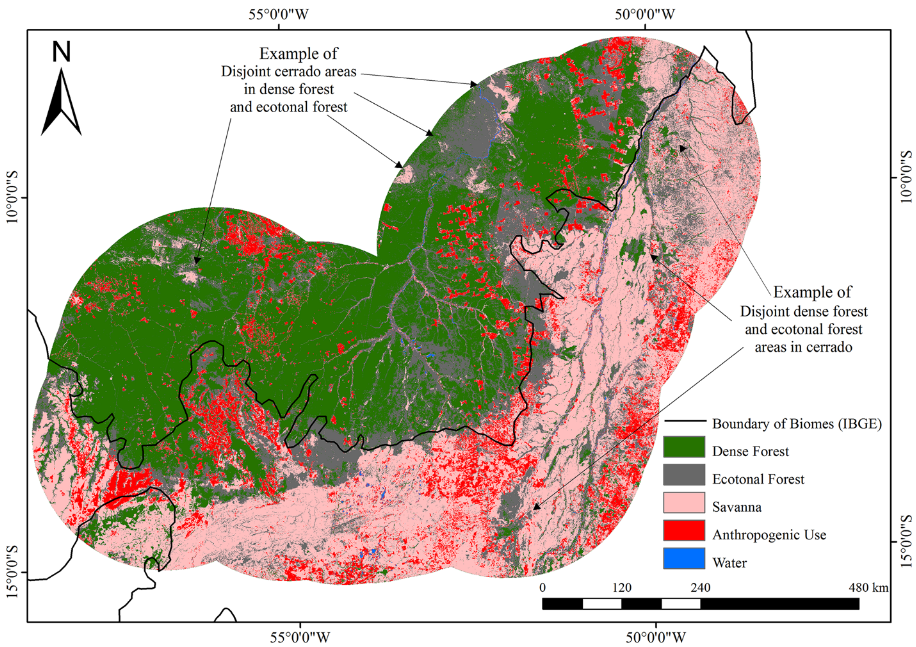

Fig. 2 Land cover classes and the numerous disjoint savanna meanders and areas of dense and ecotonal forests in the Brazilian Cerrado–Amazonia transition in 1984. Note that the boundary of biomes according RADAMBRASIL Project (Brasil 1981) is not in agreement with the distribution of forests and savannas in the Cerrado–Amazonia transition. Arrows are indicating examples of disjoint areas of cerrado in the forest domain and forest areas in the cerrado domain

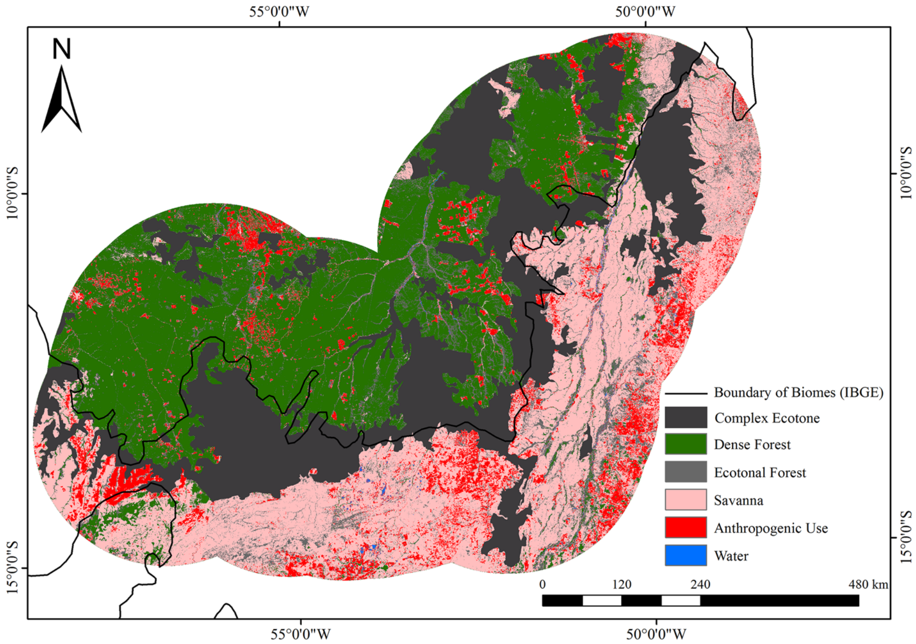

Fig. 3 Land use and land cover classification in the Brazilian Cerrado–Amazonia transition in 1984, revealing a complex ecotone (fine adjustment) where dense forests are mixed with ecotonal forests. Note that in several locations, the boundary line between biomes according to RADAMBRASIL Project (Brasil 1981) and the IBGE (2004) advances into dense and ecotonal forests, mistakenly classifying these forests as savannas

With regard to land use, our results indicate that in 1984, most deforestation took place in areas originally covered by ecotonal Amazonia-Cerrado forests. During that period, ecotonal forests, dense forests and savannas accounted for 23%, 42% and 35% of the study area, respectively (Table 1). Thirty years later, in 2014, deforestation similarly advanced into all vegetation classes of the study area (Fig. 4, Table 1). The areas classified as dense forest in this study were substantially affected by deforestation even though ecotonal forest and cerrado were proportionally the most affected and threatened classes (Table 1). As a result, over the 30 years of our analysis, the CAT suffered more deforestation than the forests and savannas in each individual biomes (Amazonia and Cerrado).

We registered approximately 75,700 km^2 of ecotonal forests (i.e., cerradão) in areas previously mapped as Cerrado vegetation (savanna) by RADAMBRASIL Project (Brasil

Table 1 Land use and land cover change between 1984 and 2014 in the Cerrado–Amazonia transition in Brazil

Class	1984 km^2 (%)	2014 km^2 (%)	Change (km^2)	Change (%)
Dense forest	233,267 (38%)	140,152 (22.9%)	−93,115	−39.9
Ecotonal forest	127,434 (20.8%)	74,933 (12.2%)	−52,500	−41.2
Savanna	191,948 (31.3%)	113,523 (18.5%)	−78,424	−40.9
Anthropic use	57,537 (9.4%)	282,352 (46.0%)	224,812	390.7
Total	613,261	613,261	–	–

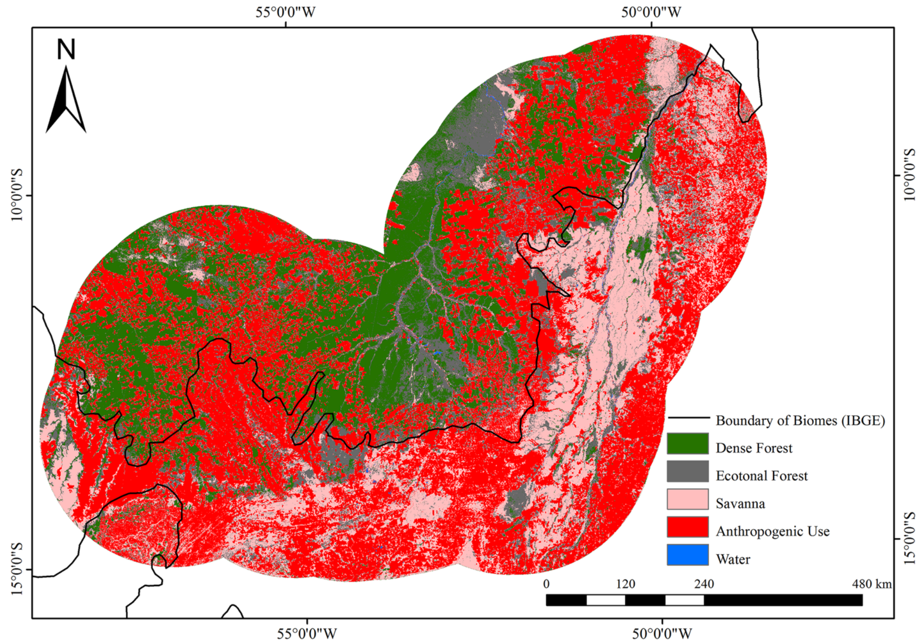

Fig. 4 Land use and land cover classes in the Brazilian Cerrado–Amazonia transition in 2014. Note the strong northward expansion of the agricultural frontier with extensive conversion of native vegetation to anthropic use where a vast area of ecotonal forests was deforested

1981), revealing the mismatches of the former savanna vs forest classification in the official mapping. The most evident case was registered in the Sorriso Municipality (Fig. 5), the largest continuous crop area in Mato Grosso State, currently comprising more than 5000 km^2 (500,000 hectares).

Discussion

Our findings also indicate that the forest-savanna boundaries of the CAT are a complex mosaic of dense and open different types of vegetation distributed throughout a vast region in southern Amazonia. Such a pattern reveals more heterogeneity in the Cerrado and Amazonian floras than previously reported in the literature and in the former mapping of the IBGE-RADAMBRASIL Project, which fail to define the limits on the ground between the two vast South American biomes. As a consequence, vegetation losses across the northern limits of the Cerrado and the southern limits of Amazonia have reached levels close to collapse in areas with intense land use for crops and pastures.

We revealed that the boundary between forests and savannas cannot be defined by a simple line but must include a complex transition zone whose width, in our study, may reach up to 250 km. Our results corroborate the pioneer field descriptions of vegetation in southern Amazonia conducted by Soares (1953), Ratter et al. (1973) (Brazil-UK Xavantina/Cachimbo expedition) and Ratter et al. (2003). We also corroborate more recent field

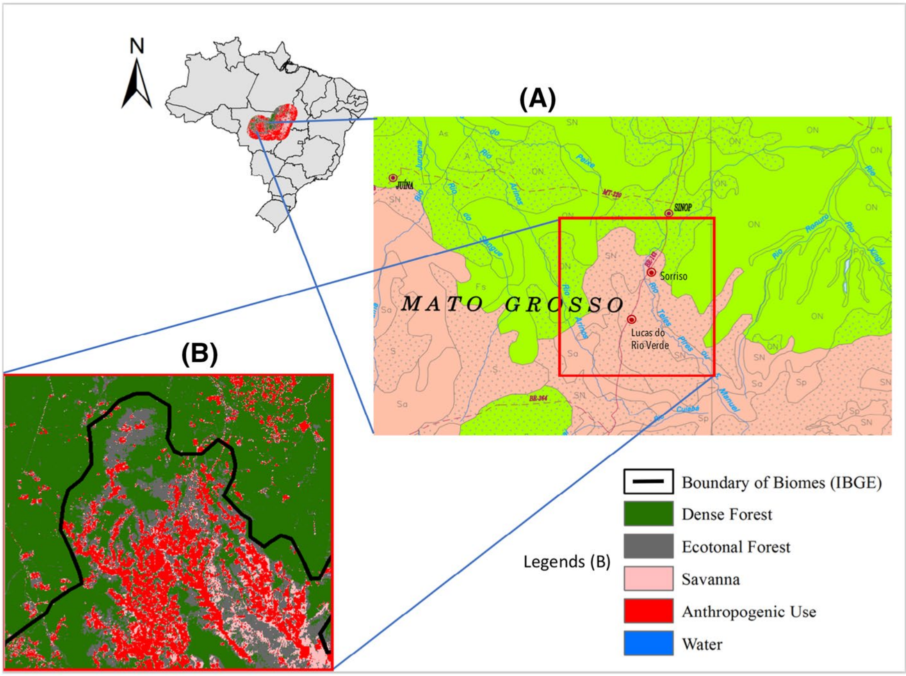

Fig. 5 Part of the original IBGE vegetation chart **a** (BRASIL 1981) showing the distribution of vegetation in the region of Sorriso and Lucas do Rio Verde municipalities, which did not exist at the time of the mapping (we inserted the approximate location). In **b** it is possible to note the advance of the crops (red) in the areas of ecotonal forest (grey) in 1984. In **a** *Sa* Savanna Arborizada (dense cerrado) and *SN* Contato Savana-Floresta (savanna-Forest contact). The category SN is a cartographic artifact used by IBGE to represent areas where the scale of the mapping does not allow to separate the types of vegetation (BRASIL 1981)

studies showing the floristic complexity and accelerated dynamics of vegetation in the CAT conducted by Marimon et al. (2006) and Marimon et al. (2014).

Our mapping using fine scale and the current techniques of Landsat imagery reveals that the previous official mapping of the IBGE-RADAMBRASIL, based on radar imagery and larger scale, is not accurate enough to allow public policy planning based on forest-savanna dynamics, biogeographical distribution of the flora, ecosystem functioning and the effect of land use on biodiversity across the known Arc of Deforestation of the agricultural frontier in Brazil. For example, the strong northward expansion of the agricultural frontier in Brazil from 1984 to 2014 ignored the natural boundaries of the two floras, the Cerrado and Amazonia, when considering the ecotonal forests (cerradão) as savanna vegetation rather than forests. As a result, nowadays the cerradão phytophysiognomies have not been protected in 80%, as determine the Law for forest formations, and are now close to the extinction in many areas across the CAT.

Another problem we disclose here, with the more refined scale and Landsat tools, is the underestimation of 245.5% of the extension of the boundary between Amazonia and the Cerrado, pointing out that the CAT is much more meandrous than previously proposed by the official classification (Fig. 4). Because the radar remote sensor and broader mapping scale used, the former mapping considers the CAT only as a simple and abrupt boundary line between both biomes, which does not reflect the reality of the transition area and disregards the interdigitating pattern of the contact between forests and savannas. Consequently, large areas belonging to the ecotonal vegetation of cerradão forests and their associated biodiversity were ignored as a forest formation. Therefore, cerradão forests were suppressed because of the strong northward expansion of the agricultural frontier in which farmers, cattle ranchers and loggers were able to freely convert up to 65% of the native vegetation areas into crops and pastures.

We clearly showed that the simplification of the division between the two biomes led to the deforestation of most of the ecotonal complex of the study area and consequent losses of biodiversity at high levels. For example, in the municipalities of Sorriso and Lucas do Rio Verde (State of Mato Grosso), most of the areas originally mapped by IBGE as "dense cerrado" and "cerrado-forest contact" (Fig. 5a) are in fact ecotonal forests (cerradão), therefore being less protected by the legislation, which permit up to 65% of deforestation in savanna areas of the Amazon legal domain (EMBRAPA 2013). With this scenario of allowing deforestation up to 65% of these forest areas, soybean expanded rapidly towards the Amazon biome through corridors of ecotonal forests (Fig. 5b), which were easier and safe to convert to crops compared to the dense forests.

Recent studies on native vegetation emphasize the CAT complexity, indicating that it can comprise greater local biodiversity than each biome separately (Marimon et al. 2006; Mews et al. 2012; Marimon et al. 2014). It is clear that the width of the CAT varies greatly throughout its length, considerably increasing the difficulty in establishing a line between them and exposing unique ecotonal forests to the fragility of the law and the consequent struggle to preserve peculiarities and fine variations of the vegetation and its associated fauna. These current scenarios reveal that the boundary between the largest and richest savanna and tropical forest in the world is not only threatened due to climate change, deforestation, burning and logging but also due to a lack of precise mapping and definition of particular ecotonal vegetation. Such inconsistencies in the mapping affect not only the southern boundary of Amazon but also the Cerrado biome, which is considered one of the most important terrestrial world hotspots for conservation priority since Mittermeier et al. (1998).

Nevertheless, our mapping reveals that the complex mosaic of vegetation in the CAT, composed of savannas, ecotonal forests (Marimon et al. 2006; Marimon-Junior and Haridasan 2005), gallery forests and hyperseasonal flooded savannas (Marimon et al. 2012), can be related to environmental diversity of the region. For instance, several environmental factors, such as soil fertility, moisture and texture (Marimon-Junior and Haridasan 2005), topography, relief and hydrography, converge to create high habitat diversity (Brasil 1981). This singular condition of phytogeography was first reported in the classic fieldwork conducted by Ducke and Black (1953), who described forest intrusions into the Cerrado and disjoint savanna sites within Amazonia, which are now confirmed in fine scale by our mapping.

A possible explanation for such vegetation complexity in the CAT is the historical dynamics of retraction and expansion of forests and savannas in response to climatic fluctuations in the late Pleistocene and Holocene. This condition was first proposed by Ab'Sáber (1958) and later corroborated by other researchers such as Pessenda et al. (2001), who analyzed soil $\delta^{13}C$ signatures with ^{14}C dating and reported the occurrence of repeated periods of vegetation changes during the lower and middle Holocene caused by climate fluctuations. Savanna-type vegetation dominated the southern Amazonia region during the last 18,000 ^{14}C year BP but changed from 6400 and 5300 14C year BP to forest-type vegetation, with a marked increase in palms (*Mauritia* and *Mauritiella*) during the last ca.

3500 ^{14}C year BP (Behling and Hooghiemstra 2000). Most of the paleovegetation surveys in Amazonia indicate a possible forest encroachment into savanna in response to a hotter and wetter climate. Fluctuations in temperature were also indicated by speleotherms in a cave in the Peruvian Amazon, where the average temperature was ~ 17 °C for the beginning of the Holocene, which are much lower than the current average at the same site (~ 22 °C) (Breukelen et al. 2008).

The dynamics of the advancement and retraction of forests and savannas indicate several climate variations driving the savanna-forest shifts from the last glacial maximum (LGM) to the present (Appendix Fig. A4). Even across the long periods of climate stability before the LGM, the biota could be influenced by savanna-forest boundaries. For example, Werneck et al. (2012), evaluating fauna distribution, suggested several savanna corridors and refuge areas of forests in the northeastern Cerrado that contributed to the biogeographical patterns during the dry periods of the LGM and last interglacial. Under the current climate conditions, the forest flora distributions in the CAT is related to soil moisture (Marimon-Junior and Haridasan 2005;) and watersheds variations (Morandi et al. 2016b), since the southern border of Amazonia corresponds exactly to a transition from CwA (wetter) to Aw (drier) Köppen climate (Alvares et al. 2013) and to the watershed domain from both Cerrado and Amazonia biomes. These factors apparently enables savannas and dense forests to coexist, forming the vast floristic complexity found in the CAT, with a singular geographical distribution pattern of Amazonia and Cerrado floras as a result of late Pleistocene and Holocene climatic fluctuations and related ecological interactions, including here the influence of indigenous people on the tree species distribution (see Levis et al. 2017).

Changes in climate in both biomes seem to be continuous and occur in shorter periods of geological and ecological times. For instance, Gloor et al. (2013) pointed an increasing trend in annual rainfall during the last century in Amazonia, principally during the rainy season, but with fast reductions in the south and southeast. There were two recent short-term periods of extreme drought in 2005 and 2010, which have brought an increase in research awareness (Marengo et al. 2011), followed by the last intense drought that occurred in 2016 (Peixoto et al. 2018). These events suggested that droughts may have become more frequent in southern Amazonia (Gloor et al. 2013). The most intense drought events occur when *El Niño* matches the drought stage of the long-term cycle, such as the 1992 (Davidson et al. 2012) and the 2005 and 2010 droughts (Lewis et al. 2011), which are followed by strong heat waves. These events, apparently related to global warming, suggest a long-term change in the hydrological regime in the forest (Gloor et al. 2013), which may cause shifts in the natural dynamics of savannas and forests due to acceleration in the frequency and duration of drought events. This situation leads us to take into account the need for a more accurate mapping of flora distribution in the CAT, as proposed in the present work. This kind of mapping study, along with climate studies, biogeography and ecological modeling, can contribute to better predict the future scenarios of a changing climate in the region and its effects on biota.

We also have to consider fire as another important factor influencing actual biodiversity conservation (Alencar et al. 2004; Silvério et al. 2013). Burning in the forests and savannas of the CAT intensify during drought events as a consequence of anthropic actions. Even though the savannas comprise vegetation evolutionarily more adapted to fire, more frequent burnings can lead to the degradation of the Cerrado (Hoffmann and Jackson 2000). Likewise, frequent droughts can increase the frequency of burnings and synergically lead forest environments to savannization (see Silvério et al. 2013).

Droughts, fires and uncontrolled deforestation occurring at the same time in the Brazilian Agricultural Frontier, also known as the "Deforestation Arc", reveal a scenario of imminent collapse of biodiversity in the CAT if climate change and land misuse persist. The most threatened type of vegetation in this altered landscape is ecotonal forests because they are more susceptible to deforestation and conversion compared to dense forests (Alencar et al. 2004). Ecotonal forests present a higher decrease in cover due to conversion to anthropic use between 1984 and 2014, resulting in a highly fragmented landscape, with nearly 41% of ecotonal forests converted into crops and pastures. Such a condition leads to a collapse of the connectivity between Amazonia and the Cerrado and, consequently, increasing biodiversity losses as a consequence of isolation of those remnants (Metzger 2006), thus compromising biodiversity in both biomes.

The conversion of natural savanna areas into crops and pasture (40.9%) was similar to ecotonal forests (41.2%). This pattern reflects the current legislation, which establishes a larger legal reserve area for Amazonia. The IBGE mapping indicates the region located between the great crop-producing cities of Lucas do Rio Verde, Sorriso, Tapurah, Ipiranga do Norte and Vera (Fig. 5) as part of the Cerrado biome; consequently, a nearly 65% deforestation was legally authorized. However, this region clearly belongs to the CAT, presenting a mixture of forests and savannas where *cerradão* ecotonal forest formations previously dominated as a class of vegetation (Table 1). The new Brazilian Forest Code establishes that rural properties located in Amazonia must preserve 80% of the native vegetation, while only 35% must be protected in the Cerrado. Indigenous lands and conservation units account for only 16.7% of the total mapped area in our study (Appendix Fig. A5). If it were not for indigenous lands (e.g., Xingu Indigenous Park) and conservation units such as Araguaia State Park, the Cerrado and other open vegetation would be less protected than forests. According to Overbeck et al. (2015), biodiversity conservation in Brazil has prioritized forests and given less attention to ecosystems such as savannas, *pampas*, and *campos de murundus* (mound fields), among others.

Another important issue is the unique and rare types of vegetation recently described in the CAT, such as *Brosimum rubescens* monodominant forests, whose remnants represent a minimum fraction of their original cover (Marimon et al. 2001). Mesotrophic *cerradão* forests (sensu Ratter et al. 1973) are also a rare type of vegetation and are virtually extinct in the region. We can still cite the flooding forests (da Silva et al. 2018), hillside vegetation, *impucas*, saline formations of *carnaúba* palm (Brasil 1981), valley forests on mesotrophic soils (derived from carbonate rocks) (Ratter et al. 1973), Araguaia *caatingas of paleodunas* (Pacheco and Oliveira 2016) and forest bi-dominated by *Dacriodes* and *Sacoglottis* (Marimon et al. not published). All these formations are a few examples of undescribed but already-threatened vegetation types across the Cerrado-Amazonia transitional belt. Unfortunately, it is not possible to map the exact area lost by those types of vegetation owing to the elevated degree of deforestation.

Those patterns are most likely also true in southeastern and northeastern Amazonia, where similar contact between both biomes exists, as well as in other savanna-forest contacts throughout the world, which stresses the urgency to fill the knowledge gaps throughout the CAT. Such conditions highlight the need for studies on populations, communities, and ecosystem processes. We also suggest that the CAT should be urgently remapped and regulated by specific legislation because it has unique features in relation to Amazonia and the Cerrado. Likewise, the Cerrado Biome should generally be protected by more specific and effective legislation due to the high degree of threat to the biodiversity.

This biome border redefinition is important to support definition of public conservation policies focused on ecosystem processes and regional diversity. The ecosystem processes and the biodiversity complexity of this large contact zone (over 6000 km) is similar throughout the tropical regions, especially in the savanna-forest boundaries of the Central

Africa and Australia. The Arc of Deforestation is currently one of the largest agricultural frontier in the world, where most of the soybean and livestock to supply the international market is produced. Accelerated deforestation within this ecotone region may increase forest fire susceptibility, fragmentation, and edge effect, which will lead both the Cerrado (Ratter et al. 1997) and the Amazon biomes to a collapse of biodiversity and ecosystem services such as world and regional climate regulations.

Conclusion

Our results indicate that Amazonia and the Cerrado are not separated by an abrupt ecotone, as previously proposed by official mapping conducted by the IBGE. The CAT is actually a complex transition zone of varying width, composed of meanders and intrusions mainly between savanna and forest vegetation types. The length of the transition zone was miscalculated by 245.5% in some areas. Accordingly, we believe that the complexity of savanna-forest boundaries in the tropics may have been underestimated and misinterpreted in current mapping efforts. This can lead to several complications for conservation efforts, which we have noted in this study. We estimated that ecotonal forests were more deforested than dense forests, especially due to a lack of protected areas, proper mapping and specific legislation. Several ecotonal forest stretches were cleared as a consequence of the original IBGE mapping, which defined CAT areas as part of the Cerrado Biome. In this scenario, close to the imminent collapse of biodiversity, the elaboration of specific laws aimed at preserving CAT and the establishment of protected lands are crucial to guarantee its persistence and temporal maintenance of exclusive ecosystems and ecological processes in the Cerrado-Amazonia transitional zone.

Acknowledgements We thank CAPES for the MSc scholarship to the first author and the National Council of Science and Technology of Brazil (CNPq) for the financial funding of the project PPBIO 457602/2012-0 (Rede Biota do Cerrado) and productivity grants to BH Marimon, BS Marimon and GR Colli. GRC thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Conselho Nacional do Desenvolvimento Científico e Tecnológico (CNPq), Fundação de Apoio à Pesquisa do Distrito Federal (FAPDF), and the Partnerships for Enhanced Engagement in Research (PEER) program for financial support.

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