

# Recurrent wildfires drive rapid taxonomic homogenization of seasonally flooded Neotropical forests

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## SUMMARY

Recent evidence has shown that most tropical species are declining as a result of global change. Under this scenario, the prevalence of tolerant species to disturbances has driven many biological communities towards biotic homogenization (BH). However, the mechanisms that drive communities towards BH are not yet thoroughly understood. We tested effects of recurring wildfires on woody species richness and composition in six seasonally flooded Amazonian forests and whether these fires reduce species composition (i.e., taxonomic homogenization) over short periods of time. Our results show that these forests are undergoing taxonomic homogenization in response to recurring fire events. Species richness decreased as a result of local extinctions and floristic similarity increased among forest communities. Fire was selecting tolerant ('winner') species and eliminating the more sensitive ('loser') species. BH leads to biodiversity erosion, which can deeply alter ecosystem processes such as productivity, nutrient cycling and decomposition, resulting in important consequences for conservation.

**Keywords:** Amazonia, biological impoverishment, biotic homogenization, biotic distinctiveness, floristic reassembly, non-random extinction

## INTRODUCTION

Human-induced land use and climate change are having negative impacts over most of the Earth's tropical biodiversity (Sala *et al.* 2000; Berenguer *et al.* 2014). Most tropical species are declining and changing their geographical distributions

as a result of human activities, leading to biodiversity erosion processes (Parmesan & Yohe 2003). In this scenario, human-induced changes may be acting as non-aleatory filters in the selection of disturbance-tolerant species, either by survival or regeneration after disturbances (Smart *et al.* 2006; Tabarelli *et al.* 2010), and these species may gradually replace disturbance-sensitive species, thus increasing in abundance and geographical distribution. This process, known as taxonomic homogenization (TH), is part of a larger process of temporal simplification of originally different biotas and erosion of biodiversity, called biotic homogenization (BH), which also takes into account functional and genetic homogenization (Olden 2006; Olden & Rooney 2006).

The drivers of BH are either direct, such as biological invasions and species extinctions (Olden & Poff 2003; Olden 2006 and references therein), or indirect, such as urbanization (Kühn & Klotz 2006; McKinney 2006) and forest fragmentation (Lôbo *et al.* 2011). Nonetheless, the characterization of the mechanisms that drive BH is far from complete (Olden 2006). Many other degradation processes may have a relevant role in the temporal simplification of biotas, like disturbance of sensitive environments, such as wildfires in traditionally fire-free vegetation types (Barlow & Peres 2008).

Among tropical forests, seasonally flooded forests are less resilient to fire, with negative and long-term effects on vegetation structure and composition, as well as the rapid loss of soil fertility (Flores *et al.* 2017). These factors aggravate the susceptibility of these forests to the more frequent recurrence of fire due to habitat fragmentation, neighbouring agriculture or pasture management and climate change. Habitat fragmentation induces canopy openness, thus allowing for greater light incidence that favours herb entrance (grasses (Poaceae) and sedges (Cyperaceae)) and faster vegetation moisture loss, resulting in increased flammability (Cochrane *et al.* 1999; Silvério *et al.* 2013). Pasture management uses regular burning for renewing of grasses, and these fires accidentally escape to the neighbouring forests. There is also evidence of changing climate, and while in the Amazon basin the mean annual pattern of precipitation remains unchanged (Gloor *et al.* 2013), dry periods are

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becoming longer and more intense, which is resulting in an increasing occurrence of fire events (Gatti *et al.* 2014); even in the wetter years, the transitional forest in the eastern Amazon is more vulnerable to fire occurrence due to human actions in the landscape change (Alencar *et al.* 2015). Increased fire recurrence in Amazonian forests normally results in drastic changes in species composition and in forest structure and functioning (Cochrane *et al.* 1999; Cochrane & Laurance 2002; Nepstad *et al.* 2008; Davidson *et al.* 2012) and could theoretically induce TH by replacing fire-sensitive species with a small group of fire-tolerant species with the ability to survive or regenerate after fire, as well as to colonize burned environments (Barlow & Peres 2008; Veldman & Putz 2011).

There are many vegetation types that have been experiencing increased fire recurrence in recent decades in Brazil. However, seasonally flooded forests are thought to be particularly sensitive to burning, which occurs mostly during the dry season (Maracahipes *et al.* 2014). In the Araguaia floodplain (Planície do Rio Araguaia), Brazil's largest continuous flooding area at *c.* 90 000 km<sup>2</sup> (Martini 2006), the seasonally flooded forests known as *impucas* (natural forest patches scattered in earth mound grassy fields; Eiten 1985; Marimon *et al.* 2015) are a distinctive vegetation type. These forests are increasingly being affected by fires that escape from the neighbouring savannas used for grazing and are therefore regularly burnt (Marimon *et al.* 2008, 2012, 2015). In these systems, surface fires are frequent and often trigger smouldering belowground combustion, which slowly consumes the carbon stored in the soil and the trees' rooting system, resulting in very high mortality rates (Flores *et al.* 2014; Maracahipes *et al.* 2014). Field observations also show that *impucas* recurrently affected by fire normally have their seed bank and seedling community drastically reduced or even eliminated. These forests are the habitat of many animal species (Brito *et al.* 2008; Marimon *et al.* 2008), as well as connecting the extensive water network of rivers and lakes during the wet season (Martins *et al.* 2002), and therefore their conservation is of paramount importance for the hydrological balance of the region.

This study focuses on six *impucas* in the Amazonia–Cerrado transition. The aim is to investigate whether these forests are suffering from TH as a cause of recurrent wildfires in short time intervals. Specifically, we ask the following questions: (1) Are *impucas* suffering from TH as a result of recurring fire events? (2) Which are the winner and the loser species on this TH? Regarding the first question, we hypothesize that TH is rapidly occurring in these forests, and we predict that TH is driven by high mortality rates of fire-sensitive species (loser species), which are rapidly being replaced by the survival or regeneration of a few fire-tolerant species (winner species). Regarding the second question, we hypothesize that if TH is observed in such a short time scale, it will be driven by reducing the number of native species, without replacement by invasive alien or introduced species (Tabarelli *et al.* 2012).

**Table 1** Geographical coordinates and years of fire events (Neves 2015) in the studied flooding forests (*impucas*) in the Araguaia State Park, Novo Santo Antônio municipality, Mato Grosso, Brazil.

| <i>Impuca</i> | Geographical coordinates        | Years of wildfire events |
|---------------|---------------------------------|--------------------------|
| 1             | –12°09'04.2"S and –50°49'37.0"W | 2007, 2010               |
| 2             | –12°19'11.2"S and –50°44'15.6"W | 2006, 2007, 2010         |
| 3             | –12°22'49.7"S and –50°53'27.4"W | 2007, 2010               |
| 4             | –12°25'07.2"S and –50°42'32.1"W | 2006, 2007, 2010         |
| 5             | –12°28'52.4"S and –50°53'46.8"W | 2006, 2007, 2010         |
| 6             | –12°32'36.2"S and –50°44'06.6"W | 2006, 2007, 2010         |

## METHODS

### Study area

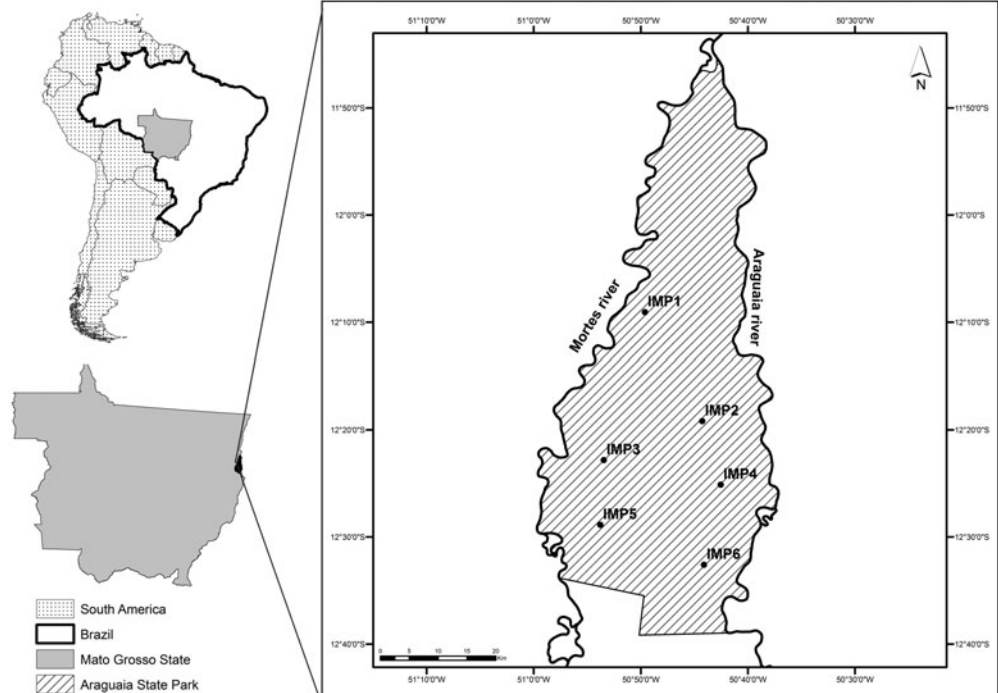
We sampled six seasonally flooded forests (*impucas*) in areas of high ecological value in the Araguaia State Park (ASP), Novo Santo Antônio municipality, Mato Grosso, Brazil (Fig. 1 and Table 1). ASP has 223 619.54 ha and is located between two important rivers, Rio das Mortes and Rio Araguaia, in the transitional area between the Amazonia and Cerrado biomes (Ratter 1987; Marimon & Lima 2001; Marimon *et al.* 2015). This is a flat region with an average altitude of 200 m above sea level on seasonally flooding and low-drainage plinthosols and gleysols (Mato Grosso 2007). The climate is classified as *Aw* Köppen, with mean annual temperatures of 25.7–27.3 °C, mean annual precipitation of 1800–2200 mm and well-defined rainy (October to March) and dry periods (April to September) (Silva *et al.* 2008).

Vegetation in ASP is composed of a mosaic of *campos de murundus* (literally 'fields of earth mounds', a type of termite savanna), *impucas*, patches of *cerrado stricto sensu* (typical savanna) and *cerradão* (dense woodland savanna) (Marimon *et al.* 2008, 2015). *Impucas* are found within a grassy mosaic and are characterized by a thick layer of litter, formed by the slow decomposition of the leaves, which favours the accumulation of fine fuel, and therefore are flammable systems (Marimon *et al.* 2008, 2012, 2015; Santos & Nelson 2013; Maracahipes *et al.* 2014). The *impucas*' vulnerability to fire is enhanced by the entrance of graminoids or sedges such as *Scleria* spp. (Cyperaceae) (Barbosa *et al.* 2011), which contribute to high fine fuel loads that dry quickly in the dry season, favouring the ignition of the litter layer and of the organic soil layer. Irrespective of annual fluctuations in the flood regime, the *impucas* always remain flooded during the rainy season because they are located in relief depressions (Marimon *et al.* 2008).

### Data collection

We inventoried six *impucas* between August 2007 and October 2008 (Time 1 – T1). At each *impuca*, we established 50 10 × 20-m plots along five parallel and transverse transects separated by 50 m. In July 2014 (Time 2 – T2), the areas were re-censused for surviving individuals, dead standing and new

**Figure 1** Geographical location of the *impucas* (IMP) studied in the Araguaia State Park, Novo Santo Antônio municipality, Mato Grosso, Brazil.



recruits (individuals who reached the minimum criteria for inclusion – see below). At each census, we recorded diameter at breast height (DBH) of all individuals (including palms and lianas) with DBH  $\geq 10$  cm in all plots. We collected botanical *vouchers* from all species that were taken to the Herbarium NX of the State University of Mato Grosso (UNEMAT, Nova Xavantina, Brazil), where all taxa was identified and verified according to the Brazilian Flora Species List (Lista de Espécies da Flora do Brasil 2015).

On the first vegetation census in 2007/2008, *impucas* 1, 5 and 6 showed evidence of fire and were occupied by *Scleria* spp. In 2014, only *impuca* 3 did not show clear evidence of fire nor presence of *Scleria* spp. Between 2000 and 2013, there were four fire events detected by satellite images (Terra/MODIS) in the area (Neves 2015; Table 1). However, not all the fire occurrences detected by the satellite reached the *impucas*, as observed in T1 in *impucas* 2, 3 and 4, which did not show signs of fire degradation. Similarly, not all fire events occurring in the *impucas* were detected by the satellites. An example of this was recorded in *impuca* 2 in 2008, when a burn occurred but was not detected by the satellite (Maracahipes *et al.* 2014). In any case, the *impucas* are surrounded by grassy fields in which fire scars can be clearly detected, even using low-resolution satellite images.

### Data analysis

To explore the potential loss of species over time, we compared species richness in the two censuses using rarefaction techniques based on number of individuals, with 1000 permutations and a 95% confidence level (Krebs 2014). To test for changes in the mean number of individuals per *impuca*

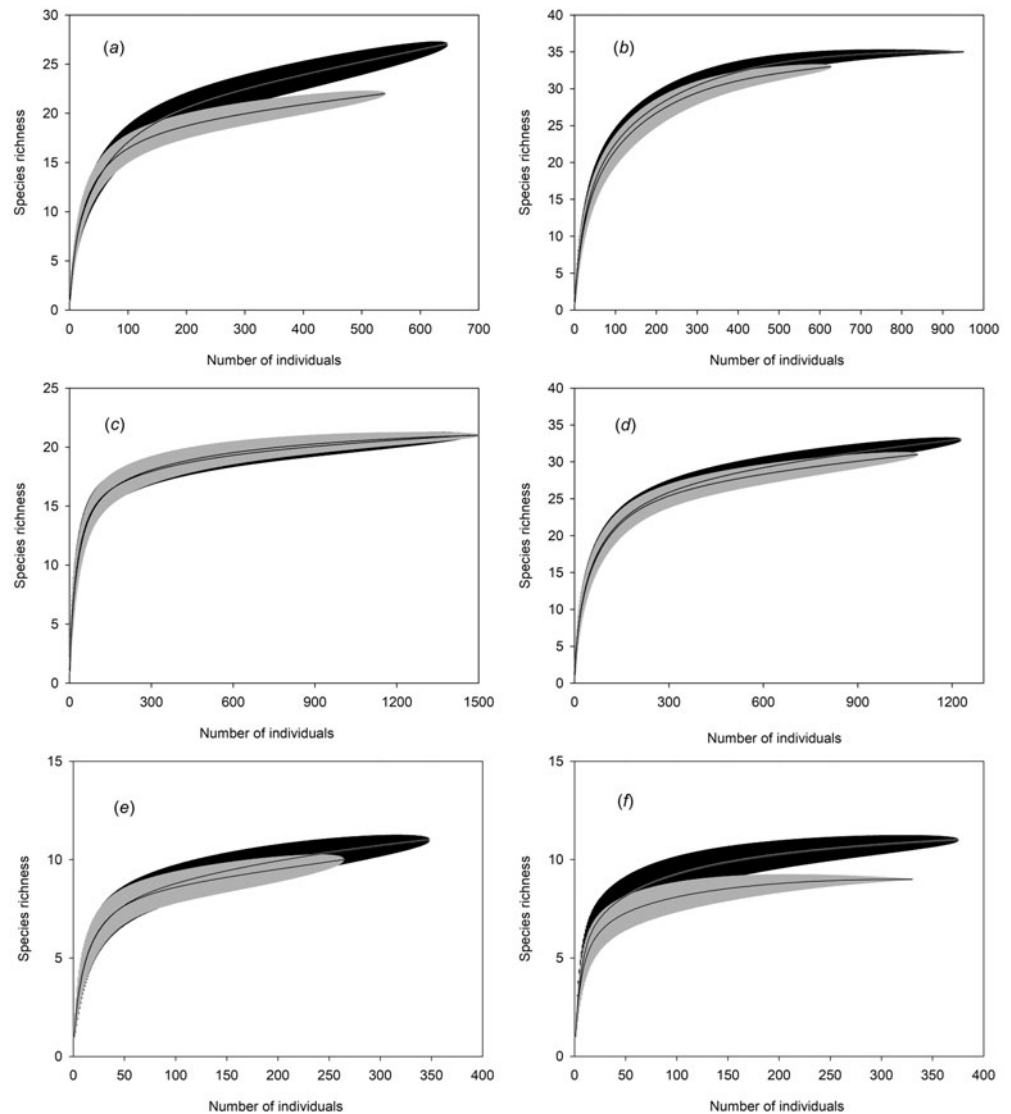
between T1 and T2, we performed paired *t* tests. To identify potential TH, we considered the species compositions at T1 and T2 and we examined the temporal variation in the similarity (using species presence or absence) with paired comparisons (Olden & Poff 2003). We used the Jaccard index to account for floristic similarity between the two periods, because this is the most common index used in BH studies (Olden *et al.* 2004). We also compared the mean similarity values between T1 and T2 using a *t* test for dependent samples. Statistical analyses were performed with PAST 2.17 (Hammer *et al.* 2001).

### RESULTS

At the six *impucas*, number of species and families varied between T1 and T2. At T1, we recorded 47 species and 29 families, while at T2, we recorded 39 species and 25 families (Supplementary Table S1; available online). Therefore, 17% of the species were lost, but the loss was not homogeneous across the *impucas*: while *impuca* 3 did not lose any species, other *impucas* lost between one and five species (Table 2). Mortality was lowest at *impuca* 3, with 6% of dead individuals at T2, and highest at *impuca* 2, with 42%. Recruitment was highest at *impuca* 5, with 21% of new individuals recorded at T2, and lowest at *impuca* 6, with only 2% (Table 2). The mean number of individuals decreased between T1 and T2 in four of the six studied *impucas* (Table 2). Species richness decreased between T1 and T2 for *impucas* 1, 2, 4 and 5 (Fig. 2(a), (b), (d) and (e)), but not for *impucas* 3 and 6 (Fig. 2(c) and (f)).

Species that had very low densities at T1, such as *Alchornea discolor*, *Eugenia* spp., *Erythroxylum anguifugum*, *Maytenus*

**Figure 2** Species richness in six seasonally flooded forests (*impucas*) sampled in the Araguaia State Park, Novo Santo Antônio municipality, Mato Grosso, Brazil, in time 1 (2007/2008, black) and time 2 (2014, grey). Black and grey bands around the central lines represent the 95% confidence intervals. (a) *Impuca* 1, (b) *impuca* 2, (c) *impuca* 3, (d) *impuca* 4, (e) *impuca* 5 and (f) *impuca* 6.



spp., *Mauritiella armata* and *Pterocarpus rohrii*, disappeared at T2 (Supplementary Table S1). The number of species present at only one *impuca* was lower at T2 and the number of species present at more than one *impuca* did not increase between censuses (Table 2 and Supplementary Table S1). These changes were more evident when we compared the species that had restricted distribution to up to three *impucas* (62% at T1 and 54% at T2). Similarly, number of species occurring in four *impucas* increased from 38% at T1 to 46% at T2 (Table 2). Among the species that occurred in four or more *impucas*, we highlight *Calophyllum brasiliense*, *Licania apetala* and *Mouriri acutiflora*, which showed an increase in their populations in *impucas* 1 and 5, in which species were lost (Supplementary Table S1).

At T1, the values of floristic similarity ranged from 0.14 to 0.70, while at T2 they ranged from 0.19 and 0.78 (Table 3). Average similarity values were higher at T2 than at T1 ( $t = 2.69$ ;  $df = 14$ ;  $p = 0.017$ ), with 73% of all possible comparisons having higher floristic similarity values at T2 (Table 3).

## DISCUSSION

Our results showed new evidence that Neotropical, seasonally flooding forests show TH and an increase in floristic similarity as a result of increased fire frequency. The role of fire as a modifying driver of tropical forests has already been recognized, and there is plenty evidence that fire reduces species richness and acts as a local extinction filter of species that are not tolerant to fire (Cochrane & Schulze 1999; Barlow & Peres 2008; Oliveras *et al.* 2014; Devisscher *et al.* 2016; Flores *et al.* 2016), as well as causing long-term shifts in forest structure and species composition of tropical forests (Pinnard *et al.* 1999; Barlow *et al.* 2003; Balch *et al.* 2008; Flores *et al.* 2014; Oliveras *et al.* 2014; Devisscher *et al.* 2016; Durigan & Ratter 2016). Given the short period of time (i.e., 7 years) between censuses and the profound differences that we found in the species composition and forest structure between the two censuses, we highlight the important role of fire as a BH agent in seasonally flooding forests.



**Table 2** Forest structure variables in the six seasonally flooded forests (*impucas*) studied in the Araguaia State Park, Novo Santo Antônio municipality, Mato Grosso, Brazil, between time 1 (T1, 2007/2008) and time 2 (T2, 2014).  $n$  = number of living individuals  $\text{ha}^{-1}$ ;  $M$  = mean of number of individuals  $\pm$  standard deviation;  $t$  test = paired comparison of the mean number of individuals between T1 and T2 in each *impuca*;  $S$  = total species richness;  $SS$  = number of shared species between the six *impucas*;  $D$  = number (and percentage) of dead individuals between T1 and T2;  $R$  = number (and percentage) of new recruits between T1 and T2;  $df$  = degree of freedom.

|          | Impuca 1                             |                | Impuca 2                             |                | Impuca 3                              |                 | Impuca 4                             |                | Impuca 5                             |               | Impuca 6                             |               |
|----------|--------------------------------------|----------------|--------------------------------------|----------------|---------------------------------------|-----------------|--------------------------------------|----------------|--------------------------------------|---------------|--------------------------------------|---------------|
|          | T1                                   | T2             | T1                                   | T2             | T1                                    | T2              | T1                                   | T2             | T1                                   | T2            | T1                                   | T2            |
| $n$      | 646                                  | 539            | 950                                  | 626            | 1467                                  | 1496            | 1227                                 | 1089           | 375                                  | 330           | 348                                  | 264           |
| $M$      | 12.9 $\pm$ 6.5                       | 10.7 $\pm$ 6.2 | 19 $\pm$ 7.6                         | 12.5 $\pm$ 7.9 | 29.3 $\pm$ 10.4                       | 29.9 $\pm$ 10.4 | 24.5 $\pm$ 7.7                       | 21.7 $\pm$ 9.0 | 7.5 $\pm$ 4.3                        | 6.6 $\pm$ 4.4 | 6.9 $\pm$ 3.7                        | 5.2 $\pm$ 4.0 |
| $t$ test | $t = 3.88; df = 49;$<br>$p = 0.0003$ |                | $t = 6.89; df = 49;$<br>$p = 0.0284$ |                | $t = -1.45; df = 49;$<br>$p = 0.1525$ |                 | $t = 3.07; df = 49;$<br>$p = 0.0034$ |                | $t = 1.65; df = 49;$<br>$p = 0.1038$ |               | $t = 6.90; df = 49;$<br>$p = 0.0010$ |               |
| $S$      | 27                                   | 22             | 35                                   | 33             | 21                                    | 21              | 33                                   | 31             | 11                                   | 9             | 11                                   | 10            |
| $SS$     | 12                                   | 7              | 8                                    | 6              | 9                                     | 8               | 11                                   | 12             | 3                                    | 1             | 4                                    | 5             |
| $D$      | 186 (29%)                            |                | 400 (42%)                            |                | 95 (6%)                               |                 | 230 (19%)                            |                | 124 (33%)                            |               | 91 (26%)                             |               |
| $R$      | 79 (12%)                             |                | 76 (8%)                              |                | 124 (8%)                              |                 | 92 (7%)                              |                | 79 (21%)                             |               | 7 (2%)                               |               |

In the Araguaia State Park, wildfires usually start at *campos de murundus* grasslands and spread into the *impucas*, especially during the dry season (Marimon *et al.* 2008, 2015). Our results suggest that a first fire event in Neotropical, seasonally flooded forests clearly causes greater mortality of individuals and that species loss increases gradually with increasing wildfire recurrence. For example, *impuca* 2 showed no signs of fire at T1 (Barbosa *et al.* 2011), but had the highest tree mortality rate of all *impucas* at T2 (42%) due to a wildfire that occurred in 2008 (Maracahipes *et al.* 2014). On the other hand, *impuca* 1, which was already degraded by fire at T1 (Barbosa *et al.* 2011) and soon after this had a new record of fire (Maracahipes *et al.* 2014), lost five plant species. Effects of fire on plant mortality have also been found recently in other types of tropical forests. For example, in *igapó* (blackwater) forests, the first fire event also caused high tree mortality and the recurrence of fire adversely affected the recovery of these forests (Flores *et al.* 2016). Likewise, in non-flooding forests of the Amazon basin, areas burned three times showed a reduction in saplings and tree species richness (Silveira *et al.* 2016), and areas burned five times showed a substantial reduction in species diversity and stem density (Balch *et al.* 2013). In other tropical forests around the world, species losses were also associated with fire (Slik *et al.* 2002; Nangendo *et al.* 2005).

The species *C. brasiliense*, *L. apetala* and *Vochysia divergens* remained common or widely distributed in the *impucas*, even in those *impucas* that had greater mortality of individuals. However, species with a narrower distribution, such as *A. discolor*, *Eugenia* spp., *E. anguifugum*, *Maytenus* sp., *M. armata* and *P. rohrii*, disappeared from several *impucas* where they had a low number of individuals (five or fewer stems) at T1. In the Amazonian Forest, 1.4% of tree species are responsible for more than half of the total number of trees, therefore being hyperdominant species (ter Steege *et al.* 2013), and these species have a higher chance of maintaining their populations after a disturbance than those with lower population sizes (Cochrane & Schulze 1999). Thus, in this context, the local extinction of the less abundant species can increase species similarity among different areas, depending on whether one common species or several species disappear (Olden & Poff 2003).

The process of BH described by McKinney and Lockwood (1999) takes into account the fact that exotic species that are highly resilient (winners) may become dominant in ecological communities after a disturbance, while most native species (losers) are not able to compete with exotic species and may become extinct. However, BH can also be the result of shifts in native species distributions after anthropogenic disturbances (Lôbo *et al.* 2011; Tabarelli *et al.* 2012; Silveira *et al.* 2016). In this case, according to the referred authors, any biotic community naturally hosts winner species that would be favoured by disturbance and loser species that would be sensitive to such disturbances. In some areas of the Atlantic Forest of the Brazilian coast, there has been a 28% increase in plant species similarity between different areas, and this similarity is driven by the increase of pioneer species in

**Table 3** Jaccard's floristic similarity matrix among six *impucas* sampled in the Araguaia State Park, Novo Santo Antônio municipality, Mato Grosso, Brazil, at time 1 (T1, lower diagonal) and time 2 (T2, upper diagonal).

|                 | <i>Impuca 1</i> | <i>Impuca 2</i> | <i>Impuca 3</i> | <i>Impuca 4</i> | <i>Impuca 5</i> | <i>Impuca 6</i> |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| <i>Impuca 1</i> |                 | 0.57            | 0.59            | 0.61            | 0.35            | 0.28            |
| <i>Impuca 2</i> | 0.48            |                 | 0.59            | 0.78            | 0.20            | 0.19            |
| <i>Impuca 3</i> | 0.45            | 0.51            |                 | 0.68            | 0.20            | 0.19            |
| <i>Impuca 4</i> | 0.50            | 0.70            | 0.59            |                 | 0.25            | 0.24            |
| <i>Impuca 5</i> | 0.41            | 0.21            | 0.19            | 0.26            |                 | 0.58            |
| <i>Impuca 6</i> | 0.27            | 0.21            | 0.14            | 0.22            | 0.57            |                 |

fragmented areas (Lôbo *et al.* 2011). Similarly, in the non-flooded forest area of the Brazilian Amazon, the compositions of birds, dung beetles and sapling species were homogenized by recurrent fire events (Silveira *et al.* 2016). Our results showed strong evidence that TH can also be modulated by fire, even in a short period of time, which favours the substitution of fire-sensitive species by fire-tolerant species, similarly to what has already been reported for tropical forests (Pinard *et al.* 1999; Barlow & Peres 2008; Balch *et al.* 2011, 2013; Oliveras *et al.* 2014; Devisscher *et al.* 2016; Silveira *et al.* 2016).

Plant mortality was higher than recruitment in five of the six studied *impucas*. This disequilibrium suggests that the effects of fire on seasonally flooding forests can last for long periods of time, as has already been found in other similar forests in the Amazon basin that still presented evidence of fire scars 19 years afterwards (Flores *et al.* 2014).

Seasonally flooded forests have a characteristic litter layer mixed by a thin, fine root matrix (Barbosa *et al.* 2011; Flores *et al.* 2014), which is particularly important for nutrient cycling (Stark & Jordan 1978). During the dry season, this organic layer dries enough to sustain surface fires that can lead to smouldering belowground combustion, consuming the roots of adult trees and therefore killing them (Flores *et al.* 2014; Maracahipes *et al.* 2014). As a result, the forest canopy opens, allowing light gaps and increasing light penetration into the forest, which in turn favours the establishment of pioneer species such as graminoids and sedges (Silvério *et al.* 2013; see also Silveira *et al.* 2016). In this study, we observed an increase of *Scleria* grass in the *impucas* in T2 with respect to T1 (data not shown). An increase in the grass biomass is directly translated into an increase in fine fuel load, which increases fire severity (Nepstad *et al.* 1999; Silvério *et al.* 2013).

With longer dry seasons and increased fire frequencies as a result of climate change (Aragão *et al.* 2008; Marengo *et al.* 2011; Gatti *et al.* 2014), seasonally flooding forests in southern Amazonia will likely suffer significant changes in their species compositions and ecosystem functioning with BH. The diversity of vegetation types in ASP demands a careful fire management plan if one aims to maintain the vegetation diversity in the area, since it is composed of a mosaic of vegetation with very different tolerance to fire, including fire thrivers and fire-tolerant and fire-intolerant vegetation communities (Pinard *et al.* 1999; Marimon *et al.* 2008, 2012, 2015; Oliveras *et al.* 2014; Pinto *et al.* 2014).

Changes in the fire regime compromise the maintenance of the ecological processes and the biodiversity of the ecosystems of the Cerrado (Pivello 2011; Durigan & Ratter 2016). The absence of fire in these environments can have a negative effect through the homogenization of the vegetation mosaic that makes up the Cerrado (Durigan & Ratter 2016), as well as greater accumulation of fuel, which increases the risk to large-scale forest fire-sensitive ecosystems (Pivello 2011).

We conclude that seasonally flooding forests can experience TH over short periods of time if fire frequency is high. Therefore, fire is an important driver of the process of TH in Neotropical forests surrounded by savanna vegetation or pastures.

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#### CONFLICT OF INTEREST

None.

#### ETHICAL STANDARDS

None.

#### Supplementary material

To view supplementary material for this article, please visit <https://doi.org/10.1017/S0376892918000127>.

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