



## RESEARCH ARTICLE

# Tropical riparian forests in danger from large savanna wildfires

Bernardo M. Flores<sup>1,2</sup> | Michele de Sá Dechoum<sup>2,3</sup> | Isabel B. Schmidt<sup>4</sup> |  
 Marina Hirota<sup>1,2,5</sup> | Anna Abrahão<sup>1,6</sup> | Larissa Verona<sup>1</sup> | Luísa L. F. Pecoral<sup>1</sup> |  
 Marcio B. Cure<sup>2</sup> | André L. Giles<sup>1,7</sup> | Patrícia de Britto Costa<sup>1,8,9</sup> |  
 Matheus B. Pamplona<sup>10</sup> | Guilherme G. Mazzochini<sup>1</sup> | Peter Groenendijk<sup>1</sup> |  
 Géssica L. Minski<sup>2</sup> | Gabriel Wolfsdorf<sup>1,7</sup> | Alexandre B. Sampaio<sup>11</sup> | Fernanda Piccolo<sup>1</sup> |  
 Lorena Melo<sup>1</sup> | Renato Fiacador de Lima<sup>3</sup> | Rafael S. Oliveira<sup>1,8</sup>

<sup>1</sup>Department of Plant Biology, University of Campinas, Campinas, Brazil; <sup>2</sup>Graduate Program in Ecology, Federal University of Santa Catarina, Florianópolis, Brazil; <sup>3</sup>Department of Ecology and Zoology, Federal University of Santa Catarina, Florianópolis, Brazil; <sup>4</sup>Department of Ecology, University of Brasília, Brasília, Brazil; <sup>5</sup>Department of Physics, Federal University of Santa Catarina, Florianópolis, Brazil; <sup>6</sup>Institute of Soil Science and Land Evaluation, University of Hohenheim, Stuttgart, Germany; <sup>7</sup>Graduate Program in Ecology, University of Campinas, Campinas, Brazil; <sup>8</sup>School of Biological Sciences, University of Western Australia, Perth, WA, Australia; <sup>9</sup>Graduate Program in Plant Biology, University of Campinas, Campinas, Brazil; <sup>10</sup>Department of Mathematics, University of Exeter, Exeter, UK and <sup>11</sup>National Centre for Biodiversity Assessment and Research and Conservation of the Brazilian Cerrado, Chico Mendes Institute for Biological Conservation, Brasília, Brazil

**Correspondence**

Bernardo M. Flores  
 Email: mflores.bernardo@gmail.com

**Funding information**

Coordenação de Aperfeiçoamento de Pessoal de Nível Superior; Instituto Serrapilheira, Grant/Award Number: Serra-1709-18983; Fundação Grupo Boticário de Proteção à Natureza, Grant/Award Number: 1114-20181; Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Number: 18/01847-0 and 2016/25086-3

**Handling Editor:** Cécile Remy

**Abstract**

1. Tropical savannas are known for the fire-prone ecosystems, yet, riparian evergreen forests are another important landscape feature. These forests usually remain safe from wildfires in the wet riparian zones. With global changes, large wildfires are now more frequent in savanna landscapes, exposing riparian forests to unprecedented impact.
2. In 2017, a large wildfire spread across the Chapada dos Veadeiros National Park, an iconic UNESCO site in central Brazil, raising concerns about its impact on the fire-sensitive ecosystems. By combining remote sensing analysis of Google Earth images (2003–2019) with detailed field information from 36 sites, we assessed wildfire impacts on riparian forests. For this, we measured the structure of trees, saplings and herbaceous plants, as well as topsoil variables.
3. Since 2003, all riparian forests had canopy cover above 90%, but after 2017, canopy cover dropped to 20% in some forests, indicating large variation in wildfire damage. A closer look in the field revealed that, on average, the wildfire killed 52% of adult trees and 87% of tree saplings in flooded forests. In non-flooded forests, impacts on adult trees were negligible, but fire killed 75% of tree saplings. Opportunistic vines and the invasive grass *Melinis minutiflora* were already present in severely disturbed flooded forests. In all forests, impacts on many ecosystem variables were related to canopy damage, a variable measurable from satellite. Overall, seasonally flooded riparian forests were the most severely impacted, possibly due to the relatively thinner barks of their trees.

4. *Synthesis and applications.* Our findings reveal how riparian forests embedded in tropical savanna landscapes are in danger from large wildfires. The destruction of some forests has opened space for new plant species that may propel a shift to an alternative ecosystem state. Riparian forests are habitat of large savanna animals and their loss could affect entire trophic networks. Managing wildfires and invasive grasses locally is probably the best strategy to maintain riparian forests resilient. As wildfire regimes intensify in tropical savanna landscapes, our findings stress the need for an integrated management that considers riparian forests as a vulnerable element of the system.

#### KEYWORDS

Cerrado, climate change, drought, global change, invasive grasses, resilience, resistance, tropical ecosystems

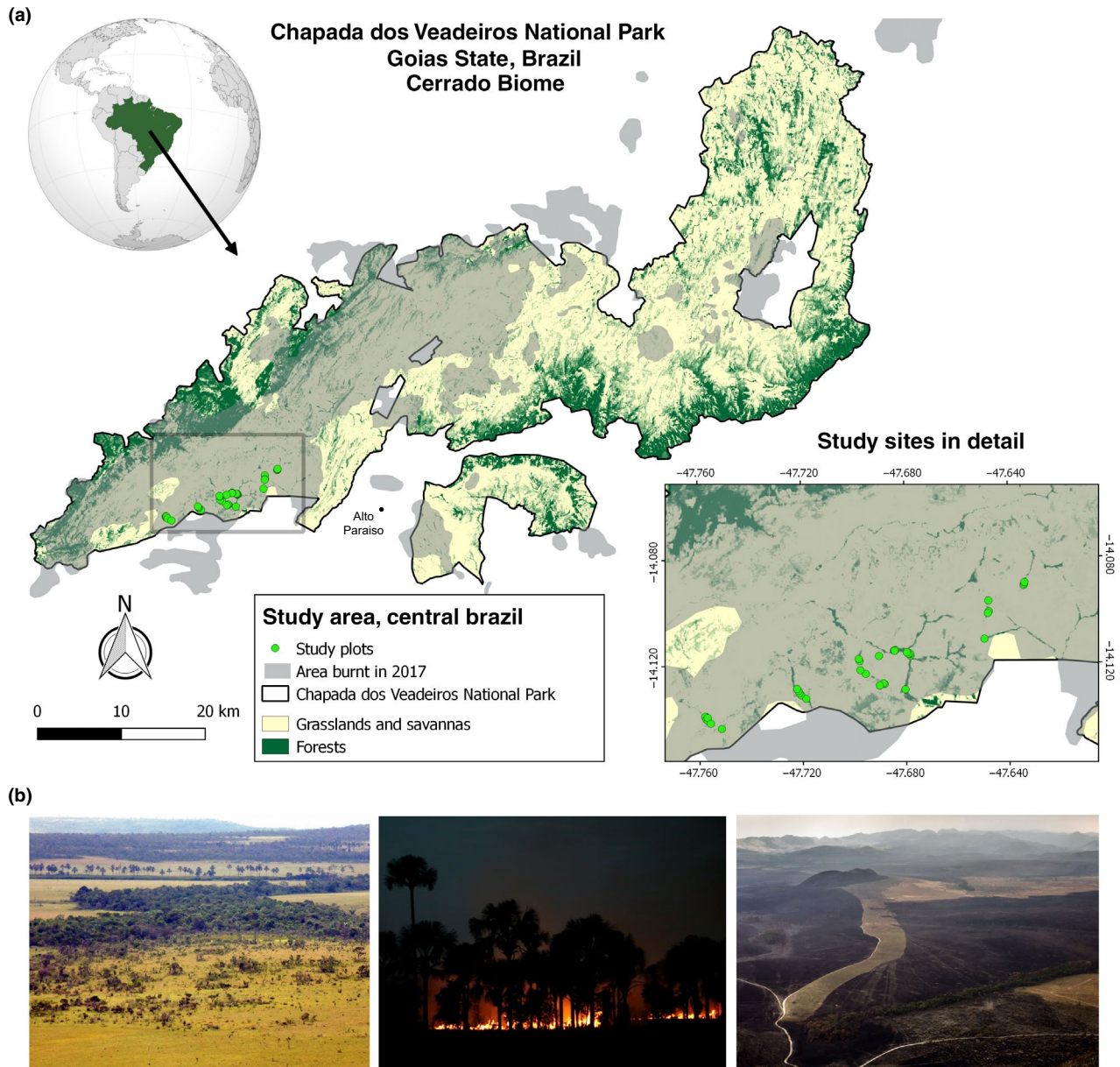
## 1 | INTRODUCTION

Globally, interactions between climate change and human activities are exposing tropical ecosystems to new stressing conditions (Barlow et al., 2018). Arguably, tropical savanna landscapes are among the most threatened, in part because of misinformed land management. Agribusiness expansion over savannas is often associated with habitat loss and the introduction of non-native grasses (Strassburg et al., 2017; Veldman et al., 2015). These grasses disperse from planted pastures and become invasive in well-preserved sites, where they often outcompete native species, altering ecosystem functioning (Damasceno et al., 2018; Zenni et al., 2019). They produce more fuel biomass than native grasses, increasing the risk of large wildfires (Damasceno et al., 2018; D'Antonio & Vitousek, 1992; Fusco et al., 2019). In addition, fire exclusion practices are also increasing landscape flammability (Schmidt et al., 2018; Veldman et al., 2015). As a result, tropical savannas are losing resilience to withstand climatic changes, with potentially negative ecological and societal consequences (Bengtsson et al., 2019).

Tropical savannas are well-known for their biodiverse open habitats dominated by fire-resistant plant species. However, fire-sensitive evergreen forests are another important feature of these landscapes, often restricted to wet riparian zones (Bueno et al., 2018; Kellman & Meave, 1997; Natta et al., 2002; Pettit & Naiman, 2007; Ribeiro & Walter, 2008). Combined, these ecosystem mosaics provide numerous services for societies. Grasslands and savannas provide forage for herbivores, medicine and wild food for local peoples, and contribute to the recharge of underground water reservoirs (Bengtsson et al., 2019). Riparian forests reduce soil erosion, enhancing water quality and water security (Wantzen et al., 2006). They may act as fire breaks, reducing the spread of wildfires (van Nes et al., 2018). Vertebrate species also benefit from the water and shelter provided by riparian forests, including top predators (Redford & Fonseca, 1986). Therefore, by connecting forest habitats and providing vital resources for keystone species, riparian forests contribute to stabilize trophic networks, and enhance the

overall resilience of tropical savanna landscapes (Estes et al., 2011). Although riparian forests are surrounded by fire-prone ecosystems, their humid microclimate and wet soils usually suppress wildfires (Hoffmann et al., 2012). As a result, most tree species are fire-sensitive, with relatively thin barks, compared to trees in the open savanna (Dantas & Pausas, 2013). However, when rare large wildfires spread during extreme drought events, they are more likely to penetrate riparian forests with potentially negative impacts (Pettit & Naiman, 2007).

In recent decades, tropical savannas world-wide have been experiencing a lengthening of the fire weather season (Jolly et al., 2015). In tropical South America, the season is now 33 days longer than 35 years ago, which implies a higher wildfire risk (Jolly et al., 2015). In 2017, a delayed onset of the rainy season, coupled with land conflicts, resulted in numerous wildfires throughout Brazil (Fidelis et al., 2018). A particularly large one spread across the iconic Chapada dos Veadeiros National Park (CVNP), burning not only savannas but also the fire-sensitive riparian forests (Figure 1; Figures S1 and S2; Text S1). Here, we combine satellite image analysis with detailed field assessments, to quantify the impact caused by this large wildfire to riparian forests of the CVNP. First, to confirm the actual timing of the wildfire and assess its damage to forest cover, we used very high spatial resolution Google Earth images (2003 through 2019, ~0.5 m), and produced a time series of canopy cover change for 16 riparian forest fragments. We then tested if wildfire damage to the canopy, measured from satellite, was a good predictor of impacts on other ecosystem variables. Using field data from 36 sites randomly spread across the study area (Figure 1), we measured the structure of adult trees and saplings, the cover of herbaceous plants, and several topsoil variables. We expected to find that canopy damage was related to tree size and bark thickness distributions; traits previously shown to influence tree mortality (Balch et al., 2011; Cochrane, 2003). Moreover, we hypothesized that in the open burnt sites, invasive grasses and opportunistic plants would be expanding, and that topsoils would be changing due to ash deposition and erosion processes.



**FIGURE 1** The 2017 wildfire at the Chapada dos Veadeiros National Park. (a) Map of the study region, in Central Brazil, showing in green forested areas, in grey the area affected by the wildfire, and in light green circles, our field study sites. (b) Photos show: (left) savanna landscape with riparian forests and palm swamp savannas along streams; (centre) fires at night, burning riparian ecosystems; (right) landscape burnt by wildfire, except for a fire break. Photo credits to B.M. Flores (left) and F. Tatagiba (ICMBio) (centre and right)

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

We studied flooded and non-flooded riparian forest ecosystems at the CVNP, Brazil (Figure 1). The landscape is formed by mosaics of different vegetation types (Ribeiro & Walter, 2008). Wet and dry grasslands and savannas occur in between streams, covering most of the landscape. At the northwest edge of the park, dry deciduous forests are found, whereas at the southwest edge, riparian evergreen forests are most common (Figure 1a). Riparian forests are closed-canopy ecosystems, which largely contrast to

the open palm swamp savannas, locally known as *veredas*. Along riparian zones, the vegetation alters abruptly between closed-canopy flooded forest and open palm swamp savannas, where native grasses coexist with the large monodominant palm *Mauritia flexuosa*. Some riparian forests in our study area can be seasonally flooded by streams in the wet season, whereas others remain above the water level throughout the year (hereafter flooded and non-flooded forests). The region receives a mean annual rainfall of 1,500 mm, has a mean dry season of 130 days, and a mean temperature of 21°C (Oliveira & Marquis, 2002). The park is surrounded by rural areas with pastures as the main activity, and small touristic towns.

## 2.2 | Google Earth image analyses

To obtain a first overview of the actual damage caused by the 2017 wildfire on riparian forests of the CVNP, we analysed time series of canopy cover produced with Google Earth images (Image data: ©2020 CNES/Airbus & Maxar Technologies) of very high spatial resolution (~0.5 m), freely available for different years in Google Earth Pro software v 7.3.3.7699. Images prior to 2013 had 1.5 m spatial resolution. We included images from 2003, 2014, 2015, 2016, 2017 and 2019, which had good quality (few clouds) for visual inspection and detection of canopy cover. To quantify canopy cover, we first used the image from 2014 to create polygons delimiting the contours of 16 riparian forest fragments within the study area (Figure 1). We classified each fragment as flooded or non-flooded, according to the micro-shed to which they belonged (Table S1). Among all riparian forests in the study area, 54% is seasonally flooded, whereas the other 46% does not flood in the wet season. We then added a spatial grid of points, spaced by 0.0001 degrees (~11 m), totalling 7,425 sample points within 90 ha of riparian forest (Figure S3). For each sample point, in each year, we visually classified as covered by forest (1) or non-forest (0), from a viewpoint of 1.5 km in height. We classified areas with bare ground, shrub or herbaceous vegetation as non-forest. For each year, we calculated canopy cover as the proportion of points inside each fragment that were covered by forest. This method has proven effective for detecting disturbances in the Amazon forest (Flores et al., 2014), which was confirmed at the CVNP. We analysed canopy cover change over the 16-year period using a 'loess' smoother with the 'GGPLOT2' package (Wickham, 2016), in R software (R Core Team, 2019).

## 2.3 | Field sampling

Six months after the wildfire, in April 2018, we sampled 36 field plots of 20 m × 10 m (0.02 ha) in riparian forests spread across five micro-sheds (streams) within the CVNP burnt area (Figure 1; Table S1; Figure S3a). With Landsat 8 (OLI) imagery from 29 January 2017, scene 221-070, using false colour composites with the bands 7 (SWIR-2), 5 (NIR) e 4 (red) and the channels red, green and blue, we first identified 82 micro-sheds that could be used in the study. Among those possibilities, we chose five micro-sheds based on two criteria: (a) that they were embedded in the landscape affected by the wildfire and (b) their accessibility (Figure 1a). The plots were spaced by at least 30 m within forest fragments in each micro-shed, avoiding stream channels and edges. Riparian forests in four of the five streams are seasonally flooded (flooded forests). In contrast, forests along one stream are not flooded because the river channel is at least 2 m deep, keeping the forest soil well-drained even in the rainy season (non-flooded forests). Among the 36 study sites, six were located in unburnt forests, including one in the non-flooded area and five in flooded areas. These sites were considered our ground reference for the pre-fire state. The other 30 study sites were located in

forests burnt by the 2017 wildfire, including eight in non-flooded forests, and 22 in flooded forests. We classified forests as burnt or unburnt in the field using fire signs, such as charred trees and ashes in the superficial soil. We also confirmed our classification with Google Earth, using three sample points for each field site, to analyse their canopy cover change in time series.

In each 20 m × 10 m field plot, we measured the diameter at breast height (1.3 m, DBH) of all trees ≥10 cm. We also measured tree bark thickness using a bark corer. Because bark thickness increases with tree age, we worked with relative thickness, calculated as  $100 \times (\text{thickness}/\text{DBH})$ , according to Lawes et al. (2013). Moreover, in three evenly spaced positions along the 20 m central line of each plot, we dug trenches to measure root mat depth, including fine roots and hummus. In these same trenches, beneath the root mat, we collected superficial soil samples (0–20 cm) that formed one single compound sample per plot. These soil samples were analysed for texture and available (exchangeable) nutrients at the Soil Department Laboratory at the Federal University of Viçosa, Brazil (see Text S2 for details).

For each 20 m × 10 m field plot, we fixed four subplots of 1 m × 1 m in each corner, in which we sampled tree saplings, native herbaceous cover, native vine cover, non-native (exotic) grass cover, bare soil cover and canopy cover. All measures taken from the four subplots were averaged to produce a single value per plot. In each subplot, we measured the density of woody saplings with DBH between 1 and 5 cm. We visually estimated the cover of herbaceous plants, vines and non-native grasses within one of seven classes; class-0 for 0% cover, class-1 for cover 0%–5%, class-2 for cover 5%–25%, class-3 for cover 25%–50%, class-4 for cover 50%–75%, class-5 for cover 75%–95% and class-6 for cover 95%–100%. We also visually estimated bare soil cover from 0% to 100% in each subplot, considering bare soil as the absence of root mat, litter or living plants. We estimated canopy cover using a Lemmon Spherical Concave Densimeter, taking measures to the north, south, east and west from each subplot, at 1.2 m above the ground. We obtained a total of 16 canopy cover measures per 20 m × 10 m field plot, which we averaged to obtain a single estimate.

## 2.4 | Field data analyses

Our analyses involved three main steps: (a) detect canopy cover changes over 16 fragments (~90 ha) of riparian forest; (b) test if fire damage to the canopy, measured with satellite and in the field, was a good predictor of other impacts on vegetation and soil variables measured in the field; (c) test if fire damage could be explained by tree diameter and bark thickness.

Step 1 involved a landscape-scale analysis to understand the magnitude of the 2017 wildfire. This approach also allowed us to extrapolate our field observations. We validated our remote sensing analysis by comparing canopy openness measured with Google Earth (image of 2019) with canopy openness measured in the field (in 2018), in both cases after the wildfire. Satellite estimates were

based on observations from the three sample points nearest to each field plot (see Figure S3). Field estimates of canopy openness were based on 16 observations per plot. We used a Pearson correlation analysis to compare both estimates of mean canopy openness.

For step 2, first we quantified mean fire impacts on the vegetation and topsoil in field sites. For this, we first divided values found in burnt forests, by the mean value of unburnt reference forests:  $(1 - \text{'burnt-site'}/\text{'reference-mean'}) \times 100$ ; (in the case of non-flooded forests, we used the values from the single reference site). For each variable, based on the impact observed in burnt sites, we estimated means and 95% confidence intervals. We then assessed in detail whether canopy openness could be used as proxy for other ecosystem impacts. This hypothesis is consistent with previous studies, showing that severe fires cause high tree mortality in tropical forests, increasing canopy openness and consequently the risk of reburning, grass invasion and topsoil erosion (Brando et al., 2014; Cochrane, 2003; Flores, Staal, et al., 2020). We related 'canopy openness' with tree basal area, sapling density, native and non-native herbaceous cover, vine cover, bare soil cover, root mat depth, as well as soil texture and nutrient availability. We analysed our data using linear mixed models (LMMs) with the R package 'lme4', function 'lmer' (Bates et al., 2015). For each response variable, we used 'canopy openness' as a fixed factor, and 'micro-shed' as a random factor, to control for landscape heterogeneity (Table S1). As a complementary analysis, we compared fire impacts between burnt and unburnt flooded and non-flooded forests, again using the function 'lmer' (Bates et al., 2015), with 'forest type' as fixed factor and 'micro-shed' as a random factor. We visually analysed the residual-plots from each model to check for normality, and log-transformed the variables: 'sapling density', 'native vine cover' and 'P concentration', to approach normal distribution. For all analyses, we tested for spatial autocorrelation using the function 'correlog', in the R package 'nCF' (Bjornstad, 2020), with distance classes of 0.005 degrees (~550 m). We did not find any spatial autocorrelation among our field study sites in any of the analyses (Figures S4 and S5), and thus assumed that all field sites were independent replicates. Due to an imbalance in the number of replicates for flooded and non-flooded forests (Table S1), we compared burnt forests of the single non-flooded micro-shed, with burnt forests grouped in four flooded micro-sheds. For this group comparison, we used the nonparametric Mann-Whitney (Wilcoxon) test, with the function 'wilcox.test' in R software (R Core Team, 2019), which uses ranked data and hence is rather robust to imbalanced sample sizes.

To understand whether tree diameter and bark thickness could explain differences in wildfire damage between flooded and non-flooded forests, we analysed the density distributions of DBH and relative bark thickness for all trees in each forest type, using data from unburnt forest reference sites only. We compared both forest types using a Mann-Whitney test with the function 'wilcox.test' in the R software. Both traits have been shown to influence fire resistance (Balch et al., 2011; Cochrane, 2003).

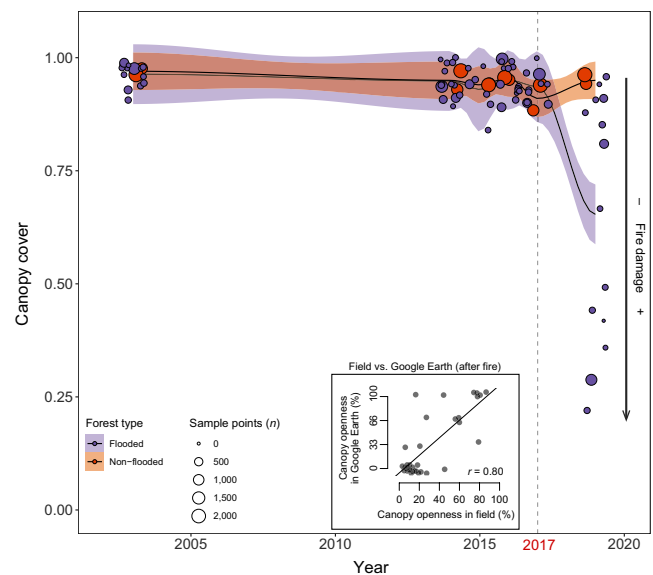
### 3 | RESULTS

#### 3.1 | Wildfire damage to the canopy from satellite

Our analysis of canopy cover change in riparian forests at the CVNP, using Google Earth imagery, suggests that at least since 2003, canopy cover in all 16 forest fragments remained high above 90%. After 2017, however, canopy cover decreased in many forests, reaching 20% in some cases, and showing that wildfire impacts varied from mild to highly destructive. Wildfire damage to the canopy varied according to the micro-shed where forests are located (Figure S6), and also to the local flooding conditions (Figure 2). We found a striking difference between flooded and non-flooded forests, with the first appearing to be more fire-sensitive (Figure 2). We validated our satellite estimates in the field, and found that post-fire canopy openness measured with Google Earth and in field plots were strongly correlated ( $r = 0.80$ ; Figure 2). Moreover, the analysis of canopy cover in the 16 forest fragments, before and after the wildfire, demonstrated how the damage was unrelated with pre-wildfire levels (Figure S7).

#### 3.2 | Wildfire impacts assessed in the field

Field assessments show that (Table 1), on average, in flooded forests, the wildfire decreased canopy cover by  $38 (\pm 13)\%$ , killed 52



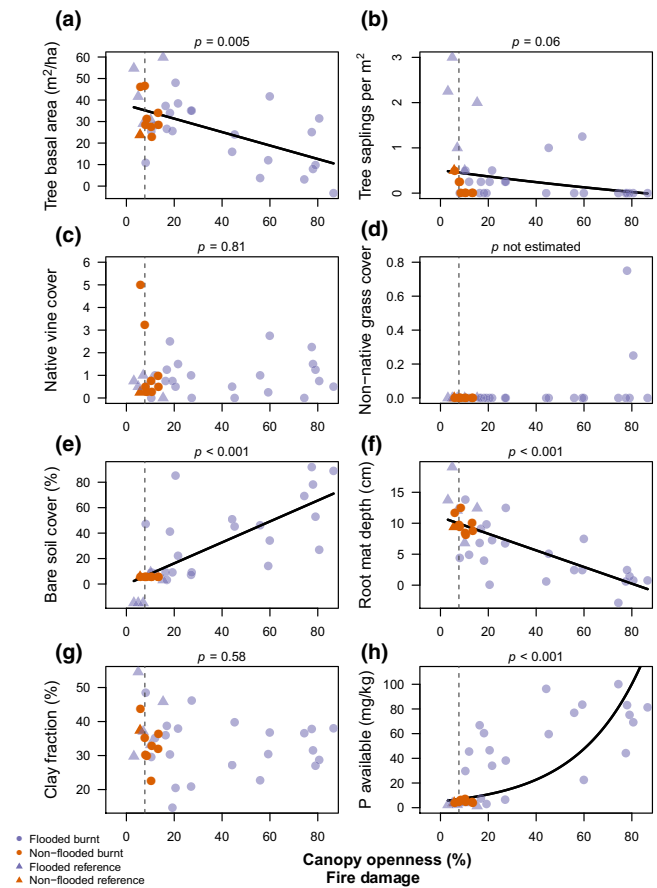
**FIGURE 2** Temporal changes in canopy cover on 16 forest fragments in the study area (~90 ha), from 2003 through 2019, derived from Google Earth images. Before 2017, canopy cover was generally high, above 90%, but after the 2017 wildfire (vertical grey dashed line), canopy cover became variable, revealing a gradient of fire damage. We applied a small jitter to the horizontal (year) axis to reduce data overlap. Inner plot shows the correlation between canopy cover measured in the field in 2018 and canopy cover measured with Google Earth in 2019. For details on sampling method, see Figure S3. Satellite image credits to Google Earth (Image data: ©2020 CNES/Airbus & Maxar Technologies)

**TABLE 1** Fire impacts on vegetation and topsoil variables of flooded and non-flooded riparian forests. We show per cent changes (mean  $\pm$  CI), relative to reference sites. Red downward facing triangles indicate reduction. Blue upward facing triangles indicate increase

Ecosystem variable	Change (%) after the wildfire	
	Flooded forests	Non-flooded forests
<b>Vegetation</b>		
Canopy cover	-38 $\pm$ 13 ▼	-4 $\pm$ 2 ▼
Tree density	-52 $\pm$ 15 ▼	+4 $\pm$ 17
Tree basal area	-47 $\pm$ 13 ▼	+83 $\pm$ 53 ▲
Sapling density	-87 $\pm$ 9 ▼	-75 $\pm$ 26 ▼
Native herbaceous cover	+20–25 ▲	+20–45 ▲
Native vine cover	+0–5	+20–25 ▲
Non-native grass cover	+0–5	0
<b>Topsoil</b>		
Root mat depth	-65 $\pm$ 18 ▼	+4 $\pm$ 11
Bare soil cover	+39 $\pm$ 14 ▲	0
Clay fraction	-25 $\pm$ 9 ▼	-17 $\pm$ 16
Silt fraction	+63 $\pm$ 19 ▲	-17 $\pm$ 20
Sand fraction	-10 $\pm$ 22	+45 $\pm$ 45
P concentration	+1,808 $\pm$ 473 ▲	+36 $\pm$ 20 ▲
Ca <sup>2+</sup> concentration	-6 $\pm$ 40	-59 $\pm$ 30 ▼
pH	+8 $\pm$ 6 ▲	-4 $\pm$ 4
Sum of bases	-2 $\pm$ 34	-54 $\pm$ 27 ▼

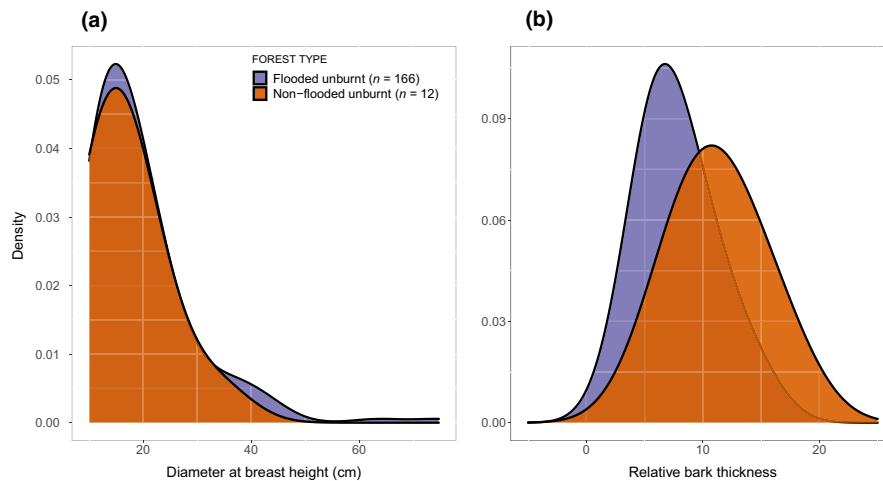
Note: Fire impacts were estimated by dividing each burnt forest value ( $N = 22$  for flooded and  $N = 8$  for non-flooded) by the forest reference mean ( $N = 5$  for flooded and  $N = 1$  for non-flooded). Confidence Intervals (CI) are based on  $\alpha = 0.05$ . The cover of herbaceous, vines and grasses changed between classes on a scale from 0 to 6, with 0 as 0% cover, 1 as 0%–5% cover, 2 as 5%–25% cover, 3 as 25%–50% cover, 4 as 50%–75% cover, 5 as 75%–95% cover and 6 as 95%–100% cover.

( $\pm 15$ )% of the adult trees and 87 ( $\pm 9$ )% of tree saplings, causing a 47 ( $\pm 13$ )% decrease in tree basal area, while native herbaceous and vine cover had increased by 20%–25% and <5% respectively. On average, invasive grasses increased <5%, but were already present in two severely burnt flooded forests. Bare soil cover increased by 39 ( $\pm 14$ )%, and root mat depth decreased by 65 ( $\pm 18$ )%. Soil clay decreased by 25 ( $\pm 9$ )%, and phosphorus availability increased by 18-fold. In contrast, in non-flooded forests, the wildfire did not significantly alter canopy cover, tree density, invasive grass cover, root mat depth, bare soil cover and soil clay. However, it killed 75 ( $\pm 26$ )% of tree saplings, increased native herbaceous and vine covers by 20%–25%, and slightly decreased phosphorus concentration. Burnt non-flooded forests also had more tree basal area than the single reference forest. These patterns and the values observed in reference forests also show how, for most ecosystem variables, wildfire impacts were severer on flooded forests, compared to non-flooded forests (Figure S8), regardless of which micro-shed they belonged to (Table S2).



**FIGURE 3** Wildfire impacts on riparian forests of the Chapada dos Veadeiros National Park. We used data on canopy openness as a proxy for fire damage. We then related canopy openness to vegetation and soil variables: (a) tree basal area, (b) tree sapling density, (c) native vine cover, (d) non-native grass cover, (e) bare soil cover, (f) root mat depth, (g) clay fraction and (h) topsoil phosphorus concentration. Field data were collected 6 months after the wildfire. The vertical grey dashed line indicates the mean canopy openness of reference sites. Statistically significant effects (based on LMM) are shown above each plot. The cover of plants in (c) and (d) varied on a scale from 0 to 6, with 0 as 0% cover, 1 as 0%–5% cover, 2 as 5%–25% cover, 3 as 25%–50% cover, 4 as 50%–75% cover, 5 as 75%–95% cover and 6 as 95%–100% cover

When then related 'canopy openness' to other ecosystem variables (Figure 3), and found that wildfire damage to the canopy significantly predicted reductions in tree basal area (Figure 3a) and root mat depth (Figure 3f), as well as increases in bare soil cover (Figure 3e) and soil available phosphorus (Figure 3h). Damage to the canopy was also significantly related to an increase in soil pH and decrease in soil aluminium (Figure S9). We found a near-significant ( $p = 0.06$ ) reduction of sapling density (Figure 3b). Native vine cover, non-native grass cover and clay fraction did not change with fire damage (Figure 3). We could not estimate changes in non-native grass cover because most sites had zero cover, although we found that two burnt sites were already colonized by the African grass species *Melinis minutiflora* (<5% cover in Figure 3d). In general, we found the strongest wildfire damages in flooded forests,



**FIGURE 4** Comparing (a) DBH and (b) relative bark thickness of individual trees in unburnt flooded and non-flooded forests. The Mann-Whitney test confirmed that both forests did not differ in terms of DBH ( $p = 0.53$ ), but were significantly different in terms of relative bark thickness ( $p = 0.002$ ). In flooded forests, we show 166 individual trees from five distinct reference sites, whereas in non-flooded forests, we show 12 trees from the single non-flooded forest site. Trees in non-flooded forests have higher relative bark thickness than trees in flooded forests, which may help explain the differences in wildfire severity

whereas non-flooded forests suffered mild damages to most ecosystem variables (Figure 3). Further analyses indicated that the cover of native vines and non-native (exotic) grasses did not change with topsoil phosphorus (P) concentration, neither with bare soil cover (Figure S10). Both sites where non-native grasses were present, however, had high P concentration.

Our analyses of density distributions of tree DBH and relative bark thickness indicated that, although trees in both forest types have similar DBH values (Figure 4a;  $p = 0.53$ ), trees in the non-flooded forests have relatively thicker barks, compared to trees in flooded forests (Figure 4b;  $p = 0.002$ ).

## 4 | DISCUSSION

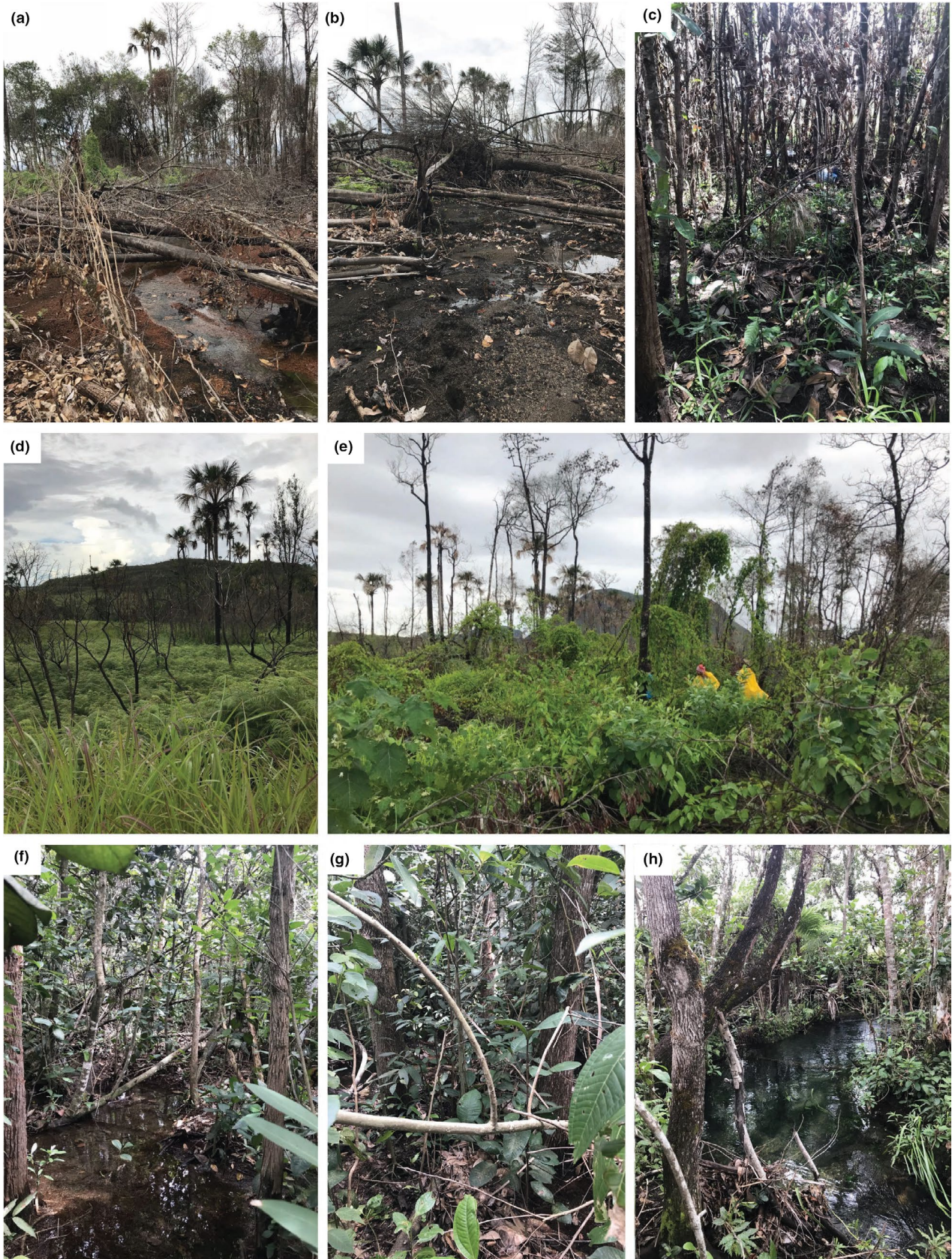
### 4.1 | Wildfire impacts on riparian forests

Our results reveal how large wildfires can be destructive for riparian forests embedded in tropical savanna landscapes. In riparian forests of the CVNP, the 2017 wildfire killed on average half of all adult trees and 88% of tree saplings. It consumed half of topsoil root mats, exposing 28% of bare soils, which boosted phosphorus availability, probably as a result of ash deposition. These impacts were stronger on seasonally flooded forests than on non-flooded forests, with some sites suffering complete mortality and topsoil combustion (Figures 3 and 5a,b). In severely burnt forests, favourable light and nutrient conditions may have facilitated the expansion of opportunistic plants, such as vines and ferns, which already covered parts of our field plots only 6 months after the wildfire (Figure 5d,e). In two of these sites, invasive grasses were already present at low covers. Overall, our findings confirm our hypothesis that riparian forests are fire-sensitive ecosystems, and indicate that seasonally flooded forests, which represent 54% of all riparian forests in this landscape,

are the most vulnerable to wildfires. Although our field assessments are imbalanced with relatively more sites representing flooded forests, our analyses were robust in suggesting their higher sensitivity, compared to non-flooded forests (Table S2).

A similar pattern has been observed in the Amazon, where seasonally flooded forests are more sensitive to wildfires than non-flooded forests (Flores et al., 2014; Nogueira et al., 2019; Resende et al., 2014). Flooding conditions are known to cause hypoxia, and trees often invest in above-ground root systems to overcome this stress (Parolin et al., 2004). Slow litter decomposition in these systems also causes humus to accumulate in the topsoil (dos Santos & Nelson, 2013). Root mats retain soil humus, reducing nutrient leaching and erosion (Stark & Jordan, 1978), while enhancing oxygen acquisition under water (Parolin et al., 2004). Yet, during the dry season of extremely dry years, root mats may act as fuel for deadly smouldering wildfires (Flores et al., 2014; Resende et al., 2014). In most tropical forests, a single wildfire usually kills between 23% and 44% of the trees (Cochrane, 2003). In floodplain forests, however, one single wildfire event can kill 60%–100% of all adult trees, which places them among the most fire-sensitive tropical forests (Flores et al., 2014, 2016; Resende et al., 2014). Our findings at the CVNP reveal that, while the non-flooded forests suffered negligible tree mortality, flooded forests suffered on average 52% tree mortality from a single wildfire event.

Root mats may have contributed to increase forest flammability during the 2017 drought. However, non-flooded forests also have root mats (Figure 3f), which raises the question of why they only suffered mild damage. Tree size and bark thickness are traits known to enhance internal protection from fire damage in tropical forest trees (Balch et al., 2011; Cochrane, 2003). We found that, while both forest types had similar DBH distributions, trees in the non-flooded forest had higher bark thickness, compared to trees in the flooded forest (Figure 4). This pattern suggests that both forest types may



**FIGURE 5** Riparian forests of the Chapada dos Veadeiros National Park after the 2017 wildfire. (a, b) Two burnt flooded forests with forest structure and organic soils severely disturbed. (c) Burnt flooded forest with low tree mortality. (d) Severely burnt flooded forest dominated by the opportunistic fern *Pteridium arachnoideum*. (e) Severely burnt flooded forest dominated by vines. (f–h) Three unburnt flooded forests



have experienced different fire regimes in the past (Pellegrini et al., 2017). Another possibility is that the thicker barks of trees in non-flooded forests are an adaptation to reduce water loss during the dry season (Loram-Lourenco et al., 2020), which contributed to increase their wildfire resistance.

## 4.2 | Post-wildfire ecosystem response

An emerging question is whether severely disturbed riparian forests will recover back to their original state or remain arrested by self-perpetuating vines, ferns and invasive grasses. In a similar tropical savanna landscape of Belize, riparian forests were shown to recover well from small wildfires (Kellman & Meave, 1997). At the CVNP, however, the 2017 wildfire was a rare event that killed most trees and saplings, and consumed most of the organic soil in some forests (Figure 3), potentially destroying tree seed banks. Remnant trees often contribute to attract animal dispersers and facilitate forest recovery after disturbances, yet, when most trees have been killed, dispersal may be limited. Even if seeds are able to arrive in burnt forests, they will have to overcome multiple recruitment limitations, such as competition with herbaceous plants (Figure 5d,e). In burnt forests, increase in soil phosphorus concentration, as well as reduction in soil acidity and toxicity may now boost the growth of opportunistic and invasive plants. In fact, 6 months after the fire, the non-native  $C_4$  grass *Melinis minutiflora* was already present in two severely burnt flooded forests (Figure 3d), probably benefiting from the improved soil conditions (Bustamante et al., 2012). Because of its high biomass and flammable compounds, the expansion of *M. minutiflora* may reduce tree seedling survival (Hoffmann & Haridasan, 2008) and enhance overall ecosystem flammability (Hoffmann et al., 2004). Hence, the spread of *M. minutiflora* and other opportunistic plants in disturbed riparian forests may contribute to arrest forest succession, as previously shown in forests of the Cerrado and Amazonia (Flores et al., 2016; Hoffmann & Haridasan, 2008; Veldman & Putz, 2011).

An alternative possibility is that *Mauritia flexuosa* palms, as well as native grass species may colonize burnt riparian forests, as these sites are connected to palm swamp savannas along streams (Figures 1b and 5). *Mauritia flexuosa* palms often survive from wildfires and increase their seed production, potentially leading to mass recruitment in burnt sites (Arneaud et al., 2017). Transitions from riparian forest to *Mauritia* swamp savanna have been shown across the Neotropics by palaeoecological evidence (Rull & Montoya, 2014). For instance, at the Venezuelan Gran Sabana region, riparian forests were replaced by *Mauritia* swamp savannas following an increase in fire activity 2000 years ago (Montoya et al., 2011). Fires initially arrested the ecosystem in a state dominated by ferns for 200 years, until palm swamp savannas expanded permanently (Rull et al., 2013). Interestingly, some of the burnt forests we studied are also dominated by the opportunistic fern *Pteridium arachnoideum* (Figure 5d), a species known

to outcompete tree seedlings and arrest forest succession (Pivello et al., 2018).

Our findings imply that, as large wildfires become more frequent in tropical savannas, riparian forests will be increasingly exposed to the risk of collapse (Scheffer et al., 2001; van Nes et al., 2018). The complete destruction of some forests (Figure 5) may open space for new plant species with contrasting functions that propel the ecosystem to an alternative vegetation state, which could potentially be: (a) a degraded state with invasive grasses and opportunistic plants or (b) a palm swamp savanna state with *M. flexuosa* and native grasses. To reduce such risk, it is necessary to manage landscape flammability. Some protected areas of the Brazilian Cerrado, for instance, have already started implementing an Integrated Fire Management program, with the use of prescribed controlled fires (Schmidt et al., 2018). Small prescribed fires act as micro-disturbances that help restore landscape heterogeneity, reducing wildfire spread (Mistry et al., 2005). The CVNP only adopted this strategy at a larger scale after the 2017 event. Additionally, the persistent control of non-native grasses is fundamental to reduce their invasion in disturbed sites. Managing wildfires and invasive grasses at the landscape scale is challenging, yet probably the best strategy to maintain riparian forests resilient. These forests are an important habitat for large animals that move across the savanna landscape (Redford & Fonseca, 1986), implying that they contribute to stabilize trophic networks (Estes et al., 2011).

In summary, our findings reveal how riparian forests embedded in tropical savanna landscapes are in danger from large wildfires. Seasonally flooded forests were the most impacted by the 2017 wildfire at the CVNP, raising concerns about whether they will recover or shift into an alternative ecosystem state. In our study area, long fire-free periods allowed grass fuel to build-up, causing wildfires to be intense and uncontrollable. In addition, a synergistic combination of climate change (Jolly et al., 2015) and environmental governance loss (Levis et al., 2020) is causing large wildfires to happen more often in savannas landscapes of the Cerrado and Pantanal, in Brazil (Mega, 2020). The most promising solution to reduce such risk probably lies in combining the ancient indigenous fire management knowledge with recent scientific discoveries (Durigan & Ratter, 2016; Mistry et al., 2005). New forms of management using prescribed fires are already being applied in many fire-prone ecosystems, restoring landscape heterogeneity and reducing the risk of large wildfires (Buisson et al., 2019; Schmidt et al., 2018). Evidence we present here contribute to these initiatives by stressing the need to consider riparian forests as a vulnerable element of tropical savanna systems.

## ACKNOWLEDGEMENTS

The work was supported by the Fundação Grupo Boticário de Proteção à Natureza, grant 1114-20181. B.M.F. is funded by São Paulo Research Foundation FAPESP grant 2016/25086-3. P.G. acknowledges FAPESP grant 18/01847-0. B.M.F., M.H., P.G. and R.S.O. acknowledge the grant from Instituto Serrapilheira/Serra-1709-18983.

A.A., A.L.G., P.d.B.C. and G.W. acknowledge the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, Brazil) Code 001. We thank the CVNP and ICMBio for logistics. B.M.F. and A.A. acknowledge Sisbio for licences 64171-1 and 43511.

#### AUTHORS' CONTRIBUTIONS

B.M.F., M.H., M.d.S.D., I.B.S., A.A., M.B.P., A.B.S. and R.S.O. conceived and designed the study; B.M.F., M.S.D., M.B.C., A.A., A.L.G., P.d.B.C., M.B.P., P.G., G.L.M., G.W., L.V., L.L.F.P., F.P. and R.S.O. collected the field data; B.M.F. and G.G.M. analysed the field data; L.V. and L.L.F.P. collected satellite data, and together with B.M.F., analysed the data. All authors contributed to result interpretation. B.M.F. led the writing and all authors contributed substantially.

#### DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.rr4xgxd72> (Flores, de Sá Dechoum, et al., 2020; Flores, Staal, et al., 2020). Satellite data are freely available from Google Earth.

#### ORCID

Bernardo M. Flores  <https://orcid.org/0000-0003-4555-5598>

Michele de Sá Dechoum  <https://orcid.org/0000-0002-3484-2498>

Isabel B. Schmidt  <https://orcid.org/0000-0001-9420-6509>

Anna Abrahão  <https://orcid.org/0000-0001-9295-2292>

André L. Giles  <https://orcid.org/0000-0002-1973-400X>

Peter Groenendijk  <https://orcid.org/0000-0003-2752-6195>

#### REFERENCES

- Arneaud, L. L., Farrell, A. D., & Oatham, M. P. (2017). Marked reproductive plasticity in response to contrasting fire regimes in a neotropical palm. *Tropical Ecology*, 58(4), 693–703.
- Balch, J. K., Nepstad, D. C., Curran, L. M., Brando, P. M., Portela, O., Guilherme, P., Reuning-Scherer, J. D., & de Carvalho, O. (2011). Size, species, and fire behavior predict tree and liana mortality from experimental burns in the Brazilian Amazon. *Forest Ecology and Management*, 261(1), 68–77. <https://doi.org/10.1016/j.foreco.2010.09.029>
- Barlow, J., Franca, F., Gardner, T. A., Hicks, C. C., Lennox, G. D., Berenguer, E., Castello, L., Economo, E. P., Ferreira, J., Guénard, B., Leal, C. G., Isaac, V., Lees, A. C., Parr, C. L., Wilson, S. K., Young, P. J., & Graham, N. A. J. (2018). The future of hyperdiverse tropical ecosystems. *Nature*, 559(7715), 517–526.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Bengtsson, J., Bullock, J. M., Egoh, B., Everson, C., Everson, T., O'Connor, T., O'Farrell, P. J., Smith, H. G., & Lindborg, R. (2019). Grasslands—More important for ecosystem services than you might think. *Ecosphere*, 10(2), e02582. <https://doi.org/10.1002/ecs2.2582>
- Bjornstad, O. N. (2020). *ncf: Spatial covariance functions*. R package version 1.2-9. Retrieved from <https://CRAN.R-project.org/package=ncf>
- Brando, P. M., Balch, J. K., Nepstad, D. C., Morton, D. C., Putz, F. E., Coe, M. T., Silverio, D., Macedo, M. N., Davidson, E. A., Nobrega, C. C., Alencar, A., & Soares-Filho, B. S. (2014). Abrupt increases in Amazonian tree mortality due to drought–fire interactions. *Proceedings of the National Academy of Sciences of the United States of America*, 111(17), 6347–6352. <https://doi.org/10.1073/pnas.1305499111>
- Bueno, M. L., Dexter, K. G., Pennington, R. T., Pontara, V., Neves, D. M., Ratter, J. A., & de Oliveira-Filho, A. T. (2018). The environmental triangle of the Cerrado Domain: Ecological factors driving shifts in tree species composition between forests and savannas. *Journal of Ecology*, 106(5), 2109–2120. <https://doi.org/10.1111/1365-2745.12969>
- Buisson, E., Le Stradic, S., Silveira, F. A., Durigan, G., Overbeck, G. E., Fidelis, A., Fernandes, G. W., Bond, W. J., Hermann, J.-M., Mahy, G., Alvarado, S. T., Zaloumis, N. P., & Veldman, J. W. (2019). Resilience and restoration of tropical and subtropical grasslands, savannas, and grassy woodlands. *Biological Reviews*, 94(2), 590–609.
- Bustamante, M. M., de Brito, D. Q., Kozovits, A. R., Luedemann, G., de Mello, T. R., de Siqueira Pinto, A., Munhoz, C. B., & Takahashi, F. S. (2012). Effects of nutrient additions on plant biomass and diversity of the herbaceous-subshrub layer of a Brazilian savanna (Cerrado). *Plant Ecology*, 213(5), 795–808. <https://doi.org/10.1007/s11258-012-0042-4>
- Cochrane, M. A. (2003). Fire science for rainforests. *Nature*, 421(6926), 913–919.
- Damasceno, G., Souza, L., Pivello, V. R., Gorgone-Barbosa, E., Giroldo, P. Z., & Fidelis, A. (2018). Impact of invasive grasses on Cerrado under natural regeneration. *Biological Invasions*, 20(12), 3621–3629. <https://doi.org/10.1007/s10530-018-1800-6>
- Dantas, V. D. L., & Pausas, J. G. (2013). The lanky and the corky: Fire-escape strategies in savanna woody species. *Journal of Ecology*, 101(5), 1265–1272. <https://doi.org/10.1111/1365-2745.12118>
- D'Antonio, C. M., & Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematic*, 23(1), 63–87. <https://doi.org/10.1146/annurev.ev.es.23.110192.000431>
- dos Santos, A. R., & Nelson, B. W. (2013). Leaf decomposition and fine fuels in floodplain forests of the Rio Negro in the Brazilian Amazon. *Journal of Tropical Ecology*, 29(5), 455–458. <https://doi.org/10.1017/S0266467413000485>
- Durigan, G., & Ratter, J. A. (2016). The need for a consistent fire policy for Cerrado conservation. *Journal of Applied Ecology*, 53(1), 11–15. <https://doi.org/10.1111/1365-2664.12559>
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pickett, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., ... Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science*, 333(6040), 301–306.
- Fidelis, A., Alvarado, S., Barradas, A., & Pivello, V. (2018). The year 2017: Megafires and management in the Cerrado. *Fire*, 1(3), 49. <https://doi.org/10.3390/fire1030049>
- Flores, B. M., de Sá Dechoum, M., Schmidt, I. B., Hirota, M., Abrahão, A., Verona, L., Pecoral, L., Cure, M., Giles, A., Costa, P., Pamplona, M., Mazzochini, G., Groenendijk, P., Minski, G., Wolfsdorf, G., Sampaio, A., Piccolo, F., Melo, L., Fiacador, R., & Oliveira, R. (2020). Data from: Tropical riparian forests in danger from large savanna wildfires. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.rr4xgxd72>
- Flores, B. M., Fagoaga, R., Nelson, B. W., & Holmgren, M. (2016). Repeated fires trap Amazonian blackwater floodplains in an open vegetation state. *Journal of Applied Ecology*, 53(5), 1597–1603. <https://doi.org/10.1111/1365-2664.12687>
- Flores, B. M., Piedade, M. T. F., & Nelson, B. W. (2014). Fire disturbance in Amazonian blackwater floodplain forests. *Plant Ecology & Diversity*, 7(1–2), 319–327. <https://doi.org/10.1080/17550874.2012.716086>
- Flores, B. M., Staal, A., Jakovac, C. C., Hirota, M., Holmgren, M., & Oliveira, R. S. (2020). Soil erosion as a resilience drain in disturbed tropical forests. *Plant and Soil*, 450(1), 11–25. <https://doi.org/10.1007/s11104-019-04097-8>

- Fusco, E. J., Finn, J. T., Balch, J. K., Nagy, R. C., & Bradley, B. A. (2019). Invasive grasses increase fire occurrence and frequency across US ecoregions. *Proceedings of the National Academy of Sciences of the United States of America*, 116(47), 23594–23599. <https://doi.org/10.1073/pnas.1908253116>
- Hoffmann, W. A., & Haridasan, M. (2008). The invasive grass, *Melinis minutiflora*, inhibits tree regeneration in a Neotropical savanna. *Austral Ecology*, 33(1), 29–36. <https://doi.org/10.1111/j.1442-9993.2007.01787.x>
- Hoffmann, W. A., Jaconis, S. Y., Mckinley, K. L., Geiger, E. L., Gotsch, S. G., & Franco, A. C. (2012). Fuels or microclimate? Understanding the drivers of fire feedbacks at savanna-forest boundaries. *Austral Ecology*, 37(6), 634–643. <https://doi.org/10.1111/j.1442-9993.2011.02324.x>
- Hoffmann, W. A., Lucatelli, V. M. P. C., Silva, F. J., Azevedo, I. N. C., Marinho, M. D. S., Albuquerque, A. M. S., Lopes, A. D. O., & Moreira, S. P. (2004). Impact of the invasive alien grass *Melinis minutiflora* at the savanna-forest ecotone in the Brazilian Cerrado. *Diversity and Distributions*, 10(2), 99–103. <https://doi.org/10.1111/j.1366-9516.2004.00063.x>
- Jolly, W. M., Cochrane, M. A., Freeborn, P. H., Holden, Z. A., Brown, T. J., Williamson, G. J., & Bowman, D. M. (2015). Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications*, 6(1), 7537. <https://doi.org/10.1038/ncomms8537>
- Kellman, M., & Meave, J. (1997). Fire in the tropical gallery forests of Belize. *Journal of Biogeography*, 24(1), 23–34. <https://doi.org/10.1111/j.1365-2699.1997.tb00047.x>
- Lawes, M. J., Midgley, J. J., & Clarke, P. J. (2013). Costs and benefits of relative bark thickness in relation to fire damage: A savanna/forest contrast. *Journal of Ecology*, 101(2), 517–524. <https://doi.org/10.1111/1365-2745.12035>
- Levis, C., Flores, B. M., Mazzochini, G. G., Manhães, A. P., Campos-Silva, J. V., de Amorim, P. B., Peroni, N., Hirota, M., & Clement, C. R. (2020). Help restore Brazil's governance of globally important ecosystem services. *Nature Ecology & Evolution*, 4(2), 172–173. <https://doi.org/10.1038/s41559-019-1093-x>
- Loram-Lourenço, L., Farnese, F. D. S., Sousa, L. F. D., Alves, R. D. F. B., Andrade, M. C. P. D., Almeida, S. E. D. S., Moura, L. M. D. F., Costa, A. C., Silva, F. G., Galmés, J., Cochard, H., Franco, A. C., & Menezes-Silva, P. E. (2020). A structure shaped by fire, but also water: Ecological consequences of the variability in bark properties across 31 species from the Brazilian Cerrado. *Frontiers in Plant Science*, 10(1), 1718. <https://doi.org/10.3389/fpls.2019.01718>
- Mega, E. R. (2020). 'Apocalyptic' fires are ravaging the world's largest tropical wetland. *Nature*, 586, 20–21. <https://doi.org/10.1038/d41586-020-02716-4>
- Mistry, J., Berardi, A., Andrade, V., Krahô, T., Krahô, P., & Leonardos, O. (2005). Indigenous fire management in the cerrado of Brazil: The case of the Krahô of Tocantins. *Human Ecology*, 33(3), 365–386. <https://doi.org/10.1007/s10745-005-4143-8>
- Montoya, E., Rull, V., Stansell, N. D., Abbott, M. B., Nogué, S., Bird, B. W., & Díaz, W. A. (2011). Forest-savanna-morichal dynamics in relation to fire and human occupation in the southern Gran Sabana (SE Venezuela) during the last millennia. *Quaternary Research*, 76(3), 335–344.
- Natta, A. K., Sinsin, B., & van der Maesen, L. J. G. (2002). Riparian forests, a unique but endangered ecosystem in Benin. *Botanische Jahrbücher*, 124(1), 55–69. <https://doi.org/10.1127/0006-8152/2002/0124-0055>
- Nogueira, D. S., Marimon, B. S., Marimon-Junior, B. H., Oliveira, E. A., Morandi, P., Reis, S. M., Elias, F., Neves, E. C., Feldpausch, T. R., Lloyd, J., & Phillips, O. L. (2019). Impacts of fire on forest biomass dynamics at the southern amazon edge. *Environmental Conservation*, 46(4), 285–292. <https://doi.org/10.1017/S0376892919000110>
- Oliveira, P. S., & Marquis, R. J. (2002). *The cerrados of Brazil: Ecology and natural history of a neotropical savanna*. Columbia University Press.
- Parolin, P., De Simone, O., Haase, K., Waldhoff, D., Rottenberger, S., Kuhn, U., Kesselmeier, J., Kleiss, B., Schmidt, W., Piedade, M. T. F., & Junk, W. J. (2004). Central Amazonian floodplain forests: Tree adaptations in a pulsing system. *The Botanical Review*, 70(3), 357–380.
- Pellegrini, A. F. A., Anderegg, W. R. L., Paine, C. E. T., Hoffmann, W. A., Kartzinell, T., Rabin, S. S., Sheil, D., Franco, A. C., & Pacala, S. W. (2017). Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change. *Ecology Letters*, 20(3), 307–316. <https://doi.org/10.1111/ele.12725>
- Pettit, N. E., & Naiman, R. J. (2007). Fire in the riparian zone: Characteristics and ecological consequences. *Ecosystems*, 10(5), 673–687. <https://doi.org/10.1007/s10021-007-9048-5>
- Pivello, V. R., Vieira, M. V., Grombone-Guaratini, M. T., & Matos, D. M. S. (2018). Thinking about super-dominant populations of native species—examples from Brazil. *Perspectives in Ecology and Conservation*, 16(2), 74–82. <https://doi.org/10.1016/j.pecon.2018.04.001>
- R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Redford, K. H., & da Fonseca, G. A. (1986). The role of gallery forests in the zoogeography of the cerrado's non-volant mammalian fauna. *Biotropica*, 18(2), 126–135. <https://doi.org/10.2307/2388755>
- Resende, A. F., Nelson, B. W., Flores, B. M., & de Almeida, D. R. (2014). Fire damage in seasonally flooded and upland forests of the Central Amazon. *Biotropica*, 46(6), 643–646. <https://doi.org/10.1111/btp.12153>
- Ribeiro, J. F., & Walter, B. M. T. (2008). As principais fitofisionomias do bioma Cerrado. *Cerrado: Ecologia E Flora*, 1(1), 151–212.
- Rull, V., & Montoya, E. (2014). *Mauritia flexuosa* palm swamp communities: Natural or human-made? A palynological study of the Gran Sabana region (northern South America) within a neotropical context. *Quaternary Science Reviews*, 99(1), 17–33. <https://doi.org/10.1016/j.quascirev.2014.06.007>
- Rull, V., Montoya, E., Nogue, S., Vegas-Vilarrubia, T., & Safont, E. (2013). Ecological palaeoecology in the neotropical Gran Sabana region: Long-term records of vegetation dynamics as a basis for ecological hypothesis testing. *Perspectives in Plant Ecology, Evolution and Systematics*, 15(6), 338–359. <https://doi.org/10.1016/j.ppees.2013.07.004>
- Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413(6856), 591–596.
- Schmidt, I. B., Moura, L. C., Ferreira, M. C., Eloy, L., Sampaio, A. B., Dias, P. A., & Berlink, C. N. (2018). Fire management in the Brazilian savanna: First steps and the way forward. *Journal of Applied Ecology*, 55(5), 2094–2101. <https://doi.org/10.1111/1365-2664.13118>
- Stark, N. M., & Jordan, C. F. (1978). Nutrient retention by the root mat of an Amazonian rain forest. *Ecology*, 59(3), 434–437. <https://doi.org/10.2307/1936571>
- Strassburg, B. B. N., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., Latawiec, A. E., Oliveira Filho, F. J. B., Scaramuzza, C. A. D. M., Scarano, F. R., Soares-Filho, B., & Balmford, A. (2017). Moment of truth for the Cerrado hotspot. *Nature Ecology & Evolution*, 1(4), 1–3. <https://doi.org/10.1038/s41559-017-0099>
- Van Nes, E. H., Staal, A., Hantson, S., Holmgren, M., Pueyo, S., Bernardi, R. E., Flores, B. M., Xu, C., & Scheffer, M. (2018). Fire forbids fifty-fifty forest. *PLoS ONE*, 13(1), e0191027. <https://doi.org/10.1371/journal.pone.0191027>
- Veldman, J. W., Buisson, E., Durigan, G., Fernandes, G. W., Le Stradic, S., Mahy, G., Negreiros, D., Overbeck, G. E., Veldman, R. G., Zaloumis, N. P., Putz, F. E., & Bond, W. J. (2015). Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment*, 13(3), 154–162. <https://doi.org/10.1890/140270>
- Veldman, J. W., & Putz, F. E. (2011). Grass-dominated vegetation, not species-diverse natural savanna, replaces degraded tropical forests on the southern edge of the Amazon Basin. *Biological Conservation*, 144(5), 1419–1429. <https://doi.org/10.1016/j.biocon.2011.01.011>

- Wantzen, K. M., Siqueira, A., Cunha, C. N. D., & Pereira de Sá, M. D. F. (2006). Stream-valley systems of the Brazilian Cerrado: Impact assessment and conservation scheme. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 16(7), 713–732. <https://doi.org/10.1002/aqc.807>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag. Retrieved from <https://ggplot2.tidyverse.org/>. ISBN 978-3-319-24277-4.
- Zenni, R. D., Sampaio, A. B., Lima, Y. P., Pessoa-Filho, M., Lins, T. C., Pivello, V. R., & Daehler, C. (2019). Invasive *Melinis minutiflora* outperforms native species, but the magnitude of the effect is context-dependent. *Biological Invasions*, 21(2), 657–667. <https://doi.org/10.1007/s10530-018-1854-5>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Flores BM, de Sá Dechoum M, Schmidt IB, et al. Tropical riparian forests in danger from large savanna wildfires. *J Appl Ecol*. 2020;00:1–12. <https://doi.org/10.1111/1365-2664.13794>