Ecosystems (2022) 25: 279–290
https://doi.org/10.1007/s10021-021-00654-4

ECOSYSTEMS

Savanna–Forest Coexistence Across a Fire Gradient

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ABSTRACT

Tropical forests and savannas can co-occur in a range of macro-environmental conditions. In these conditions, disturbances and resource availability are thought to control savanna and forest transitions, although the mechanisms involved are disputed. We hypothesized that, in Neotropical regions where fire activity is high, fire is the main factor controlling functional differences between savanna and forest, as well as their relative resistance to biome shifts. We sampled plant functional traits and soil and determined fire history, for 198 plots distributed across three landscapes with distinct fire frequencies (high, mid, and low). In each landscape, plots covered a woody cover gradient (from wooded grasslands to forests). We tested whether the sharpness and the magnitude of the functional distinction between savanna and forest were affected by fire. We also computed the environmental hyperspace (niche space) to evaluate how biome relative stability changed in relation to fire. Functional thresholds were detected only in the high and mid landscapes, where savanna and forest plots formed a multidimensional bimodal distribution in functional trait space. The stability of savannas in relation to forest increased abruptly with fire, whereas functional differences between forest and savanna increased gradually. Our results suggest that savanna can occur as an alternative vegetation state to forest where a fire burns every 18 years (on average), but higher frequencies are required for savannas to occupy large unique portions of the environmental niche space.

GRAPHIC ABSTRACT

This photo was taken and provided by Rafael S. Oliveira, one of the authors.

Key words: alternative vegetation states; cerrado; fire; functional traits; precipitation; resource availability; savanna–forest transition; soil.

Received 26 January 2021; accepted 1 May 2021;

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s10021-021-00654-4.

Authors Contributions: V.D. and J.P. conceived the project and designed the methodology. P.B.,V.D., R.O., and M.H. collected the data. All authors analyzed and interpreted the data, contributedto the writing, and approved the final version of the manuscript.

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HIGHLIGHTS

- Forests and savannas become more functionally distinct as fire activity increases.
- Fire is necessary to understand the distribution of Neotropical forest and savanna.
- The relative stability of forest and savanna changes abruptly with fire.

INTRODUCTION

Climate is the main factor regulating biome distribution at the global scale (Rosenzweig 1968; Polis 1999). However, climate alone is insufficient to explain biome distribution at the landscape scale in many regions (Bond and Keeley 2005; Dantas and others 2016; Pausas and Bond 2020). This is particularly true for tropical savannas and forests, the two largest tropical biomes (Staver and others 2011a, b; Moncrieff and others 2015). In these ecosystems, resource availability (that is, nutrients and water availability) and disturbances interact in complex ways to control vegetation distribution (Bond and Keeley 2005; Hoffmann and others 2012; Silva and others 2013; Dantas and others 2015, 2016; Staver and others 2017; Case and Staver 2018). However, the specific mechanisms through which they interact and shape biome distribution are little understood.

In savannas, a typical continuous C_4 grass layer fuels frequent fires. These fires have been suggested to be important regulators of savanna–forest stability at the local scale, especially in mesic climates (Staver and others 2011a; Dantas and others 2015). Fire top-kills tree seedlings and fire-sensitive plants, promoting grass dominance and sparsely distributed woody plants that are fire resistant (Bond and Keeley 2005; Bond 2008; Hoffmann and others 2012). This process reinforces fire-prone savannas in climatic and edaphic conditions which are also suitable for forests (Bond and Keeley 2005; Staver and others 2011a, b; Hoffmann and others 2012). Likewise, long fire-free intervals allow canopy development (and closure) leading to the crossing of the fire-suppression threshold (Hoffmann and others 2012), if soil conditions allow (for example, Silva and others 2008, 2013; Schmidt and others 2019). Beyond this threshold, shade-intolerant grasses which are the main fuel for fires, as well as fire-resistant savanna woody species, are outcompeted by forest trees resulting in forest expansion (Hoffmann and others 2012). Thus, fire–vegetation feedbacks operate both as demographic and selective agents of woody plant functional traits, promoting the structural and functional distinctions that characterize these biomes (Dantas and others 2013).

Functional differences are among the most consistent features distinguishing tropical biomes (Ratnam and others 2011; Dantas and others 2013, 2016). Each biome is dominated by species exhibiting specific functional traits, as a result of the contrasting selective processes that assembled these communities (Ratnam and others 2011; Dantas and others 2013). For instance, relative stem height and bark thickness, specific leaf area (SLA), and wood density (WD) are important traits differentiating forests and savannas, a pattern that suggests a trade-off between efficient competition for light (that is, forest species are taller and have higher SLA and WD) and fire resistance (that is, savanna species have thicker barks) (Ratnam and others 2011; Dantas and others 2013; Charles-Dominique and others 2018; Dantas and Pausas 2020; but see Hao and others 2008; Silva and others 2013). These functional differences can be used to gain insights into the mechanisms regulating biome assembly. For instance, the occurrence of abrupt functional shifts as community closure increases from wooded grassland to closed canopy forest is consistent with the idea of a fire-suppression threshold, suggesting the fire–vegetation feedback as a mechanism regulating biome dynamics (Hoffmann and others 2012; Dantas and others 2013). Thus, comparing biome differences and overlaps in terms of functional traits and environmental conditions could greatly improve our understanding of forest-savanna assembly, and provide insights into biome relative stability as well as on the existence of alternative biome states maintained by contrasting disturbance regimes (Dantas and others 2016).

Fire activity shows a typical hump-shaped relationship with precipitation (Pausas and Ribeiro 2013; van Nes and others 2018). Where precipitation levels are very high or very low, fire activity is low, and thus, other factors (for example, microsite conditions) should gain importance on the determination of savanna–forest distribution (Rossatto and others 2009; Lehmann and others 2011; Staver and others 2011a; Hoffmann and others 2012). At certain rainfall levels (mainly between 1000 and 2500 mm/y), however, fires can be frequent, resulting in the occurrence of forests and savannas as alternative vegetation states (Staver and others 2011a; Hoffmann and others 2012; Dantas and others 2016). In tropical South America, fire frequency peaks at mean annual precipitation (MAP) levels between 1600 and 2000 mm/y, decreasing toward both drier (more gradually) and wetter (more abruptly) conditions (see Figure S1 in Supplementary Material). Thus, for MAP levels lower than 1600–2000 mm/y, fire activity decreases with decreasing MAP. As a result, the relative importance of fire in explaining vegetation structure and function should become lower and lower. As a consequence, fire–vegetation feedbacks should be stronger between 1600 and 2000 mm/y than outside this range, while the functional distinction between savanna and forest should become smoother outside this range.

We here aimed to study how regional variations in fire activity influence the vegetation functional differences and relative stability between forest and savanna. We hypothesized that the functional distinctions and relative stability between savanna and forest change with increasing fire frequency due to the increasing strength of fire–vegetation feedbacks selecting extreme fire strategies. We expected a sharp functional change along the tree cover gradient in landscapes under higher fire frequency, consistent with the fire-suppression threshold hypothesis (Hoffmann and others 2012; Dantas and others 2013), but also that this change would become smoother as we move to landscapes where lower fire frequency prevails. To understand the relative stability of these biomes in response to fire frequency, we evaluated how they overlap in environmental space (climate and soil). We expected savanna stability to increase with increasing fire frequency. We also compared fire frequencies between plots that share the environmental space, to test the hypothesis that fire maintains savanna as an alternative state to forest under these conditions.

MATERIALS AND METHODS

Study Sites

Data used in this study were collected in three savanna–forest landscapes in Brazil: (1) Emas National Park, (2) the reserve of the Brazilian Institute of Geography and Statistics (IBGE; including the adjacent protected area of the Financial Administration School, ESAF), and (3) the Araripe National Forest (see Figure S2 in Supplementary Material). The climate of the three landscapes is tropical humid (Aw; Köppen 1931), with mean annual precipitation (MAP) of 1745, 1500, and 1091 mm, respectively (Cianciaruso and others 2005; Cardoso and others 2014; IPECE 2014). Both the Emas National Park and the IBGE are characterized by a marked dry season between May and September, whereas the dry season in the Araripe Forest extends from May to December. In the three landscapes, the predominant vegetation is savanna with forests and grasslands forming small patches and strips (for example, along water courses) (Oliveira-Filho and Ratter 2002; Dantas and others 2013).

The dominant soil type in both the Emas National Park and IBGE is a deep well-drained reddish Oxisols (Ramos-Neto and Pivello 2000; Quesada and others 2004; Dantas and others 2013), whereas in the Araripe Forest yellowish-red Oxisols prevail (Jacomine and others 1986). In both the Emas National Park and the Araripe Forest, these clayey soils may interweave with more sandy soils in some places.

Field Sampling

Data from the Emas National Park were collected by Dantas and others (2013), whereas the remaining data (IBGE and Araripe Forest) were sampled for this study. In each of the landscapes, the sampling was performed in plots distributed along a woody cover gradient from forests to open wooded grasslands. In the IBGE and Araripe Forest, we distributed 50 plots (10 × 5 m) within four tree cover strata (100–60%, 59–40%, 39–20%, and 19–0%; Hansen and others 2013). For each stratum, we randomly assigned 12–14 plots located between 10 and 100 m from dirty roads (that is, near roads for practical reasons, but with a certain distance to avoid potential anthropogenic influence). In the Emas National Park, 100 plots of 5 × 5 m were distributed according to time since the last fire, as technical limitations prevented the direct use of tree cover at the time (see Dantas and others 2013 for more details). All samplings were carried out during the rainy season in 2009–2011 (Emas National Park), 2014–2015 (IBGE), and 2015–2016 (Araripe Forest). Plots assigned to inaccessible areas due to legal and/or practical issues were replaced, respecting the sampling design. We also replaced plots that contained less than three woody individuals (with stem perimeter at ground level ≥ 10 cm) of less than two different species, to maintain the same criteria used in Dantas and others (2013). All plots were located in flat or slightly sloped areas, and there were no clear systematic topographic differences between forest and savanna plots.

For each plot, we identified the species of all woody plants with at least 10 cm of stem perimeter (that is, approximately 3 cm of diameter) at the ground level. For each individual, we measured plant height, stem diameter at ground level, and

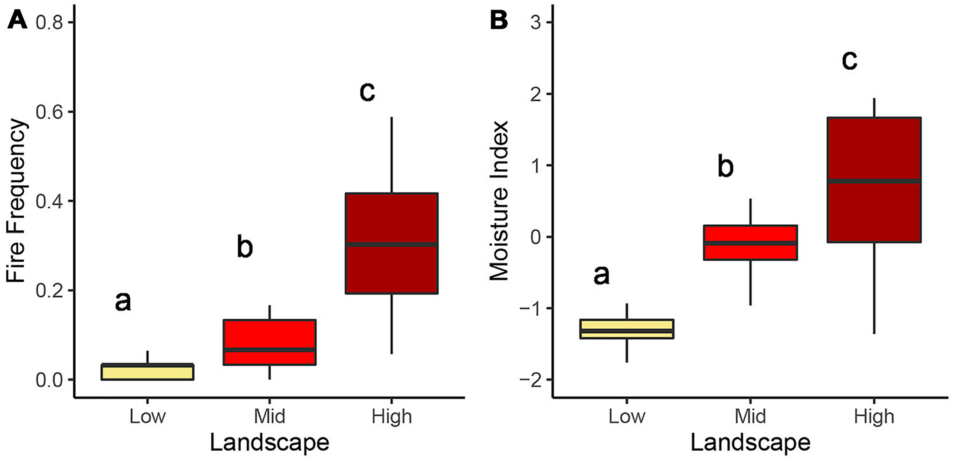

Figure 1. Fire frequency and moisture differences characterizing the studied fire activity gradient (low, mid, and high fire frequency landscapes; see Table 1 for details). Variability refers to among plots; distinct letters represent significant differences between landscapes in the (Kruskal–Wallis) Dunn's post hoc test ($p < 0.05$). Climatic and soil texture differences are presented in Figure S3.

bark thickness at 50 cm height (except for individuals bifurcating at lower heights, which were measured below the bifurcation). We also collected sun-exposed leaves and branches for further laboratory analysis. When it was not possible to reach well-exposed leaves (for example, very tall trees), samples were collected from the highest reachable branch close to the canopy surface. Using the field measurements and the leaves and branches collected, the following functional traits were derived: stem height-to-diameter ratio (relative height), bark thickness-to-diameter ratio (relative bark thickness), SLA, and WD. These are key traits marking the transition between Neotropical savanna and forest biomes (Ratnam and others 2011; Dantas and others 2013). Basal stem diameter was used to calculate the ratios. Details on how the traits were derived can be found in ''Appendix S1'' in Supplementary Material. We subsequently calculated plot-level mean trait values using all measured woody individuals of all species in each plot. In the Araripe Forest, because we only collected samples from up to five individuals for each species in each plot, we attributed the mean SLA and WD values from the sampled individuals to the remaining ones before calculating the plot-level functional traits.

In each plot, we also collected five soil samples (top 10 cm): one at each corner of the rectangular plots and one at the center. These five samples were pooled together, and the composite sample was analyzed by the Soil Science Department of the University of São Paulo (ESALQ-USP). Both physical and chemical analyses were performed (that is, phosphorus, potassium, calcium, magnesium, pH, and sand content).

Fire History

Fire history was obtained from landscape fire scars in monthly time series of Landsat imagery. The years considered depended on imagery quality and were 1979–2010 for the Emas National Park, 1985–2014 for the IBGE, and 1985–2015 for the Araripe Forest. From these images, we calculated the fire frequency for each plot during the analyzed period. Fire frequency differences were significant among landscapes, and formed a fire activity gradient (Figure 1; see ''Data analysis'' subsection), with the Emas National Park presenting higher, the IBGE intermediate, and the Araripe Forest lower fire frequency. Thus, we hereafter refer to the studied landscapes as high, mid, and low fire activity landscapes, respectively. More information about each landscape and their location can be found in Table 1.

Climate Data and Moisture Index

Based on the geographical coordinates of each plot, we obtained climate data from WorldClim (1 km spatial resolution). Specifically, we obtained precipitation data from 1970 to 2000 and calculated MAP and Rainfall Seasonality (RS; using the Walsh and Lawler 1981 index). Based on these data and soil sand content, we calculated a moisture index as the sum of the standardized (zero mean and unity standard deviation) MAP, RS, and soil sand percentages, after multiplying the latter two stan-

Table 1. Coordinates, Mean Annual Precipitation (MAP) and Soil Types of the Three Studied Brazilian Landscapes: High, Mid, and Low Fire Landscapes.

	Low fire	Mid fire	High fire
Latitude	7°10′–7°50′S	15°55′–15°57′S	17°49′–18°28′S
Longitude	39°00′–40°50′W	47°51′–47°54′W	52°39′–53°10′W
Federative unit	Ceará	Federal district	Goiás
MAP (mm)	1091	1500	1745
Soil type	Oxisols	Oxisols	Oxisols

dardized values by − 1 (to invert the positive and negative signs, so that higher values would indicate higher moisture).

Community Closure Index

To characterize the vegetation community closure (that is, woody cover) at the plot level, we calculated the community closure index (CCI). The index was calculated as the log-transformed sum of the total wood volume occupied by all individuals inside the plot, standardized to vary from zero (lowest woody cover community) to one (highest woody cover community) across the three landscapes (see Dantas and others 2013 for more details). Because plots were half the size in the high landscape, we divided the log-transformed sum of the total wood volume by two for the mid and low fire landscapes prior to performing the range standardization of CCI values across landscapes, to ensure that the CCI values (and thresholds, see below) were comparable.

Data Analysis

To confirm our assumption that the three landscapes were submitted to different fire regimes and to better characterize their overall moisture differences, we first tested for differences in fire frequency and moisture index among landscapes using a Kruskal–Wallis test followed by a Dunn's post hoc test (as data were not normally distributed). We also used a multiple regression and stepwise variable selection based on AIC to better understand how our three moisture indicators influenced fire frequency across landscapes. However, since there was strong collinearity between MAP and RS, and sand content and RS, instead of directly using these variables as predictors of fire frequency, we included these three variables in a PCA and used the two principal components that explained most of the variability in these variables. Predictor significance was tested using heteroskedasticity-consistent covariance matrix estimation. We also obtained the average variable contribution for the selected model as the mean difference in R^2 between all possible subset models with and without the targeted predictor variable, using the R package ''dominanceanalysis.''

To test whether the plot-level plant functional traits presented a threshold-type relationship with CCI, consistent with fire–vegetation feedbacks regulating plant functional trait variability (that is fire-suppression threshold, sensu Hoffmann and others 2012), we tested for the presence of breakpoints in the relationships between each trait and CCI, and compared the fit of a linear versus a piecewise model (Toms and Lesperance 2003). We tested for a breakpoint along the CCI gradient for each trait using a sup(F) test implemented by the ''strucchange'' package for R. If detected, the estimated breakpoint was used to segment the data into subsets to be used in the piecewise models, fitting separate lines to each subset. A threshold relationship was inferred by the detection of a breakpoint followed by a better fit (lower AIC) of the piecewise compared to the linear model, whereas the lack of a significant breakpoint or a better linear than piecewise fit would support a linear response to CCI. We used an ANOVA test and the corrected Akaike information criterion (AICc) to compare the models. A linear relationship was interpreted as very weak or no evidence for fire–vegetation feedback as a mechanism controlling savanna–forest assembly (Dantas and others 2013).

We also tested the hypothesis that functional distinctions between forest and savanna increased with fire frequency, consistent with fire as a key driver regulating community assembly in savanna–forest mosaics (that is, stronger filtering by stronger fire–vegetation feedback). For this, we first calculated the mean magnitude of the functional changes across all traits between forests and savannas. The magnitude for each trait was calculated as the difference between the fitted value before (first segment) and after (second segment) the breakpoint in the piecewise model (Verbesselt and others 2010). A Mann–Whitney U test was used to check if the overall magnitude of change, in plant traits that presented a significant threshold relationship with CCI, was significantly higher for one of the landscapes. To better understand these differences, we also built functional hyperspaces for each biome within each of the landscapes. For this purpose, we performed a principal component analysis on all traits and CCI, followed by hierarchical clustering, to separate the plots into two groups: savanna and forest. Based on the first two PCA axes, we then built hyperspaces for each biome and landscape and compared the environmental distances between biome space boundaries (that is, minimum distance) and centroids, and computed the environmental overlap between biomes for each landscape. These functional patterns were then compared to the environmental patterns as described below.

To understand the drivers of functional distinctions, we also computed environmental (rather than functional) hyperspaces for each biome and landscape using the functional-based classification above and PCA axes based on climate (that is, MAP and RS) and soil variables (sand percentage, phosphorus content, and the sum of bases). Because soil phosphorus and sum of bases are both drivers of—and driven by—vegetation, due to vegetation inputs in the soil organic matter pool, instead of using the measured values of phosphorus and sum of bases we used the residuals of the regression between each of these variables and soil organic matter. In all cases, we selected the two PCA axes that: (1) explained more than 10% of variability; (2) had scores significantly different between biomes in a linear model; and (3) explained the highest amount of variability in the data.

Using these axes, we built the environmental hyperspaces of each biome and landscape and computed inter-biome overlaps and distances (that is, centroid and minimum), the proportion of plots under shared hyperspaces (that is, alternative biome state plots), as well as savanna and forest relative stability for each landscape. This latter metric was calculated as the mean among three other metrics calculated for each biome and landscape: (1) proportion of the total occupied environmental space by each biome; (2) proportion of the total biome space that is exclusive to that biome (non-shared fraction of biome space); and (3) proportion of biome plots under conditions that are exclusive to that biome (see Table S1 in Supplementary Material). We assume that a biome is more stable in relation to the other when a larger proportion of the total environmental or geographical space is exclusively occupied by it, and when a larger proportion of its own space is not shared with another biome. Overlap and distance metrics were always standardized by the total size of the environmental space. Hyperspaces were calculated by thresholding (0.95) kernel density distributions using the ''hypervolume'' package for R, and represent the functional and environmental niches of biomes in each landscape (see Blonder and others (2014) for more details). Finally, we compared fire frequency between alternative biome states (that is, plots estimated to occupy conditions suitable for both savanna and forest) for each landscape using Wilcoxon tests.

All analyses were performed in the R Environment (R Core Team 2018). We log-transformed the data when necessary to improve the normality of the residuals.

RESULTS

Fire frequency, derived from remotely sensed data, was significantly different among the three landscapes (Figure 1). Fire frequency was positively correlated with the first moisture PCA axis ($R^2_{\text{adj}} = 0.20$; $p < 0.001$), which explained 80% of the variability in the moisture variables. This PCA axis was positively correlated to both mean annual precipitation (MAP; $r = 0.90$) and rainfall seasonality (RS; 0.94), and negatively correlated to soil sand percentage ($r = -0.85$; see Table S2 in Supplementary Material). The second axis, explaining 14% of the variability in moisture, was positively correlated to all moisture indicators, and did not predict variability in fire. The third axis was not considered as it explained only 3% of the variability in moisture. Overall, fire seemed to be more related to MAP than RS (Figure S4).

Functional thresholds along the community closure index (CCI) gradients were detected for all traits in the high and mid landscapes, while no threshold patterns were detected in the low (see Figure S5 and Tables S3 and S4 in Supplementary Material). The first functional trait PCA axis showed clear structural and functional distinctions between forest and savanna in the mid and high landscapes, while functional differences were less clear in the low fire landscape (Figure 2, Table 2). An overlap in savanna and forest functional traits was also clear both visually (Figure 3A) and from the functional overlap metric for the low landscape. In contrast, variability in community parameters was clearly discontinuous in the mid and high landscapes (see Table 2, Figure 2B, C). The mag-

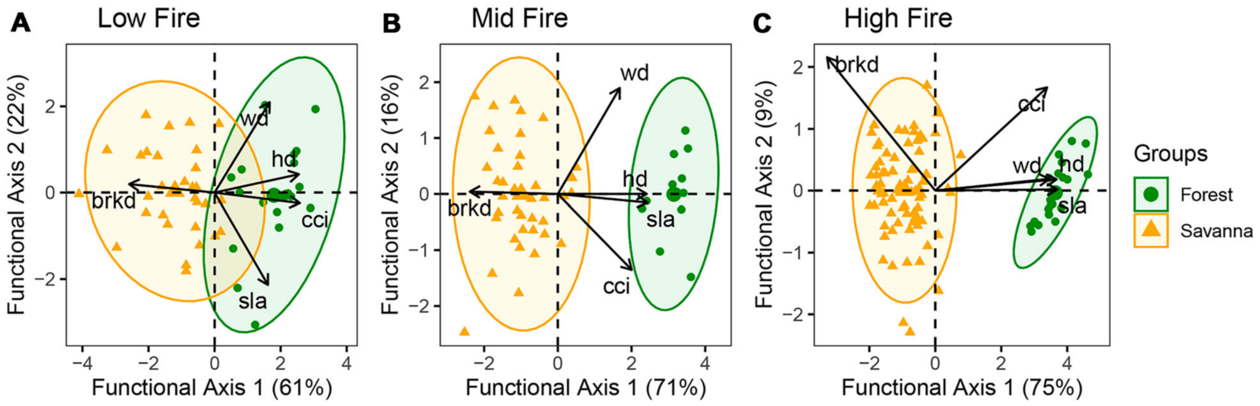

Figure 2. Functional distinctions between forest and savannas among three landscapes characterized by different fire frequencies (low, mid, and high fire, respectively). Ellipses are the 95% confidence intervals. Brkd: bark thickness-to-stem diameter ratio; cci: community closure index; hd: height-to-diameter ratio; sla: specific leaf area; wd: wood density.

Table 2. Estimated Functional Trait and Environmental Relationships Between Biomes (Forest And Savanna) and Biome Stability in Landscapes Submitted to Different Fire Frequencies (Low, Mid, and High).

Metric	Units	Low	Mid	High
Functional				
Threshold Magnitude	Index (stand. by range)	0.00	0.24	0.30
Minimal distance	Index (stand. by occup. space)	0.00	0.04	0.13
Centroid distance	Index (stand. by occup. space)	0.08	0.20	0.34
Overlap	Proportion of functional space	0.11	0.00	0.00
Environmental				
Minimal distance	Index (stand. by occup. space)	0.00	0.00	0.00
Centroid distance	Index (stand. by occup. space)	0.03	0.03	0.09
Overlap	Proportion of space	0.12	0.12	0.11
Alternative biome states	Proportion of plots	0.62	0.80	0.15
Stability				
Savanna	Index	0.11	0.04	0.79
Forest	Index	0.85	0.81	0.54

nitude of the functional thresholds along the CCI gradient was also significantly higher in the high compared to the mid ($W = 16$; $p = 0.023$; Table 3). This result was consistent with those for the minimal and centroid distance metrics, based on biome classification (hierarchical clustering) and construction of hyperspaces, which showed that functional and structural distinctions between forest and savanna increased with fire frequency (Table 2). This pattern can also be depicted from Figure 2. As expected, forests were characterized by higher relative height, SLA, and wood density, and lower relative bark thickness than savannas (Figure 2; Figure S5) in the high and mid landscapes, which presented a threshold-like functional pattern (that is, a significant breakpoint and an improved fit in the piecewise compared to the linear model).

The patterns observed for vegetation parameters did not closely match patterns for environmental hyperspaces (Figure 3; Table 2). For instance, only in the high fire landscape savannas exclusively occupied a large independent fraction of the environmental space (Figure 3). Despite the functional discontinuity between forests and savannas in the high and mid landscapes, the environmental space of savanna and forest overlapped in both cases, but especially (greater overlap) in the mid (Figure 3). In the high fire landscape, in which only a small fraction of the resource space consisted of overlaps (Figure 3), the overlap zone coincided mostly with transitional plots with intermediate CCI (Figure S5), whereas in the other two landscapes these zones were distributed along the CCI gradient (as savannas practically did not occupy an independent portion of the environmental hyperspace).

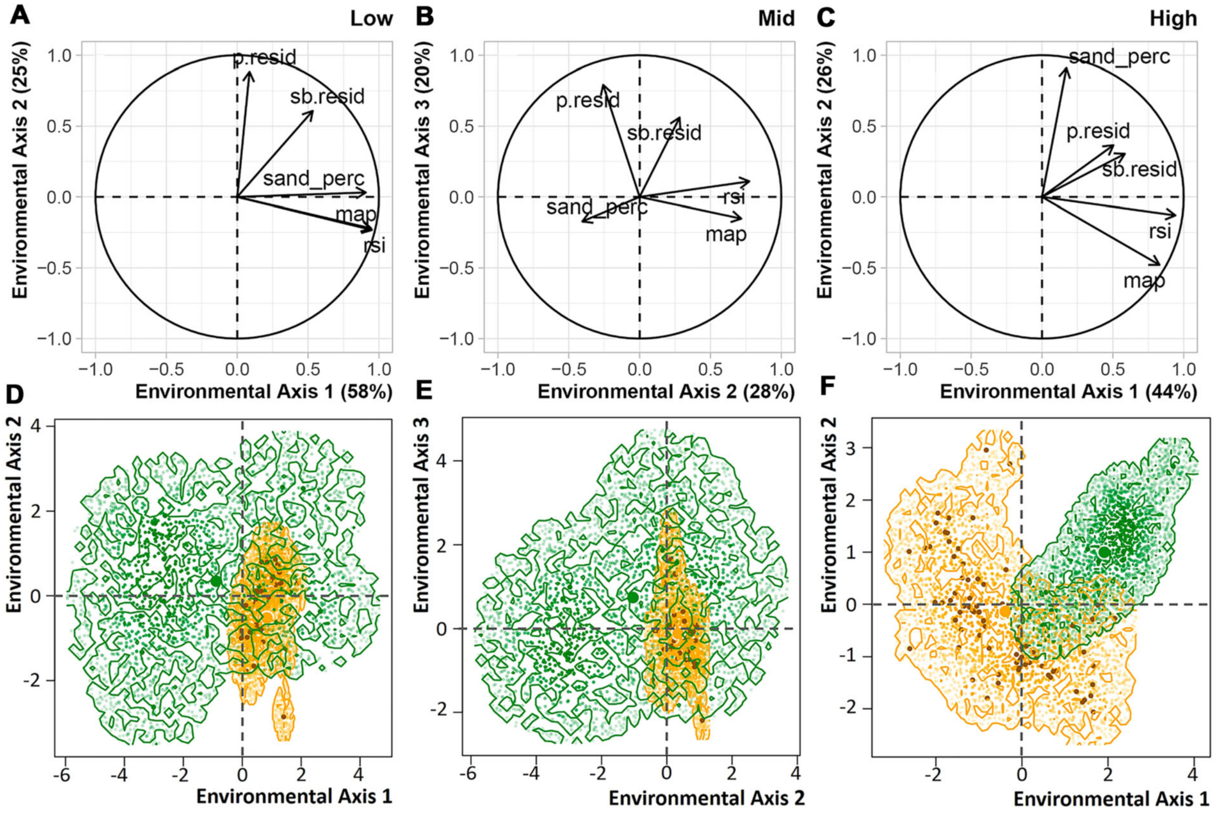

Figure 3. Environmental (that is, climate and soil) hyperspaces of forest and savanna in three landscapes with different fire frequencies: low (**A**, **D**), mid (**B**, **E**), and high (**C**, **F**). In (**A**–**C**), the environmental correlates of the principal component axes are shown on top of the corresponding environmental hyperspaces (**D**–**F**, respectively) constructed from these axes for each biome (forest in green and savanna in orange; see Figure 2). Map: mean annual precipitation; rsi: rainfall seasonality index; sand_perc: soil sand percentage; p.resid and sb.resid: residuals of the relationships of soil P and SB (respectively) with soil organic matter content (see ''Methods'').

Table 3. Mean Community Closure Index (CCI) Threshold and Standardized (by Range) Magnitude of Change of Log-Transformed Plant Functional Traits in the Savanna–Forest Transition.

Attribute	Landscape	
	Mid	High
Mean CCI threshold	0.64	0.53
Relative height	0.27	0.34
Relative stem bark thickness	0.21	0.33
Specific leaf area	0.21	0.20
Wood density	0.28	0.32

The overall magnitude (across all parameters) is significantly larger in the high fire landscape (W = 16; p = 0.023). The ''Low fire'' landscape did not show any significant threshold pattern, and thus, it is not shown

Moreover, environmental overlaps remained remarkably constant among landscapes, regardless of differences in fire frequency and moisture (Table 2). Finally, when the same distance metrics (that is, either centroid or minimal) were compared for environmental and functional parameters, the landscape in which forests and savannas showed the greatest separation in the functional trait space was not the same one in which they showed the greatest environmental space separation.

We selected forest and savanna plots located under overlapping environmental spaces to evaluate the hypothesis that fire was the main driver of the occurrence of savannas under conditions that are suitable for both forests and savannas. A significant distinction between forest and savanna fire frequency was observed in the mid and high landscapes, while no difference was observed in the low (Figure 4). Lastly, the stability metrics suggested that forests were more stable (that is, occupy large and share less environmental space) in the driest end of the gradient, where fire is rare (that is, in the low). Likewise, savannas were more stable where fire presented the highest frequency

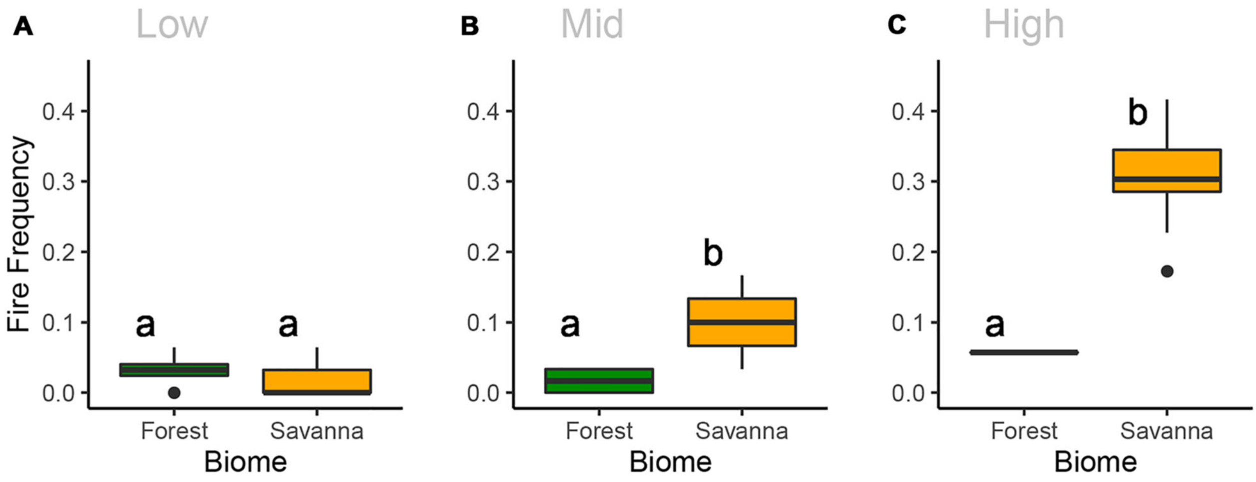

Figure 4. Differences in fire frequency between savanna and forest plots under overlapping conditions of their environmental spaces for the three landscapes subject to different fire frequencies: **A** low, **B** mid, and **C** high fire landscapes.

(that is, in the high; Table 2). These results are consistent with the hypothesis that fire, not moisture, is the main driver of the stability of forest-savanna mosaics. If precipitation was the main driver of biome stability (through a positive effect on tree cover), forest would be more stable in the high, where MAP was the highest, and less stable in the low, where MAP was the lowest. These changes in stability, however, were not linear in relation to landscape-scale differences in fire frequency (Table 2). For savannas, stability first slightly decreased from low to mid, and then increased from mid to high. Contrary, forest stability remained fairly constant from low to mid, and then decreased from mid to high.

DISCUSSION

Only in the two landscapes with highest fire frequency, functional traits showed a threshold-type relationship with community closure (Table 3; Figure S5), as predicted by the existence of a fire-suppression threshold (Hoffmann and others 2012; Dantas and others 2013). Accordingly, forest and savannas were functionally and structurally contrasting, forming opposing poles (that is, a bimodal pattern; Figure 2), as predicted by the alternative states theory (Hirota and others 2011; Dantas and others 2016; Pausas and Bond 2020). Using these distinctions to separate savanna and forest, we were able to demonstrate that the functional and structural contrasts were not well explained by climatic and edaphic conditions, as biomes greatly overlapped in functional trait space, especially where fire frequency was moderate to low. Consistent with predictions from the alternative state theory, fire frequency was completely different, even under shared portions of the environmental niche space, for the landscapes in which fire frequency was moderate to high, but not where fire frequency was low (in which a threshold was not detected). These results suggest that fire is a key factor controlling biome assembly, especially in more humid savanna–forest mosaics, maintaining savanna and forest as alternative biome states.

We showed that not only structural parameters, such as tree cover and tree basal area, but also functional parameters follow bimodal patterns. This is consistent with the idea that fire does not regulate biome distribution only by consuming vegetation biomass and driving demographic bottlenecks. By disruptively selecting for plants that either resist (that is, savanna species) or suppress (that is, forest species) fires, fire produces both structural and functional asymmetries, allowing for the recognition of forest and savanna as distinct biomes states (Dantas and others 2013; Pausas and Bond 2020). For instance, the fact that fire-resistant plants are short and fire-suppressive plants are tall could be as important to understand physiognomical distinctions between forest and savanna as fire consumption of plant biomass in savannas alone.

In the low fire landscape, in contrast, neither functional nor environmental distinctions were clearly observed, and functional changes followed a linear trend, rather than a threshold pattern, as woody cover increased. This suggests that recent fire history is unlikely to be the process determining savanna–forest distribution in this landscape, and thus, the functional changes are likely controlled by other factors (Bond 2008; Lehmann and others 2011; Staver and others 2017). The large environmental overlap between forest and savanna in this landscape and the absence of a clear functional and structural separation suggest that microsite conditions, long-term fire history, or dispersal-related processes may be more relevant than recent fire regimes (evaluated here).

Rather than linearly increasing with fire frequency, forest and savanna stability followed a stepwise pattern. That is, they presented similar stabilities in the low and mid landscapes (in the case of savanna there was actually a slight decrease), and an abrupt increase (for savanna) or decrease (for forest) from the mid to the high fire landscape (Table 2). This abrupt change was especially associated with savannas distinctively occupying a large (and forests a small) independent fraction of the environmental space in the high fire landscape (Figure 3; Table 2). This suggests a more fine and balanced partitioning of the environmental space between forest and savanna when fire activity is very high. Our results suggest that, under high fire frequency, forests tend to dominate where water availability is high (for example, high MAP; see Figure 3). In turn, under high fire frequency, savannas dominate where water availability, in general, is low, but especially where the water stays for longer in the top soil layers (for example, at low sand content).

Although changes in functional overlaps between forest and savannas were observed along the fire activity gradient, overlaps in relation to environmental hyperspaces remained surprisingly similar among landscapes (that is, approximately 11%). This suggests that, whereas the proportion of the environmental space exclusively occupied by each biome may change, the shared fraction may be governed by a universal rule. Yet, considering that only three sites were evaluated, further studies are necessary to confirm this hypothesis. According to our results, only the position of ecotones in the environmental space changed and, consequently, the proportion of the space occupied by either biome. This, however, does not imply that the amount of geographical space occupied by either biome would be the same, as this could depend on habitat availability.

Fire frequency increased both with increasing moisture and seasonality, consistent with the idea that fires are both controlled by fuel amount (MAP) and fuel moisture (RS), at least for the range considered here (MAP of 1091–1750 mm/y; Figure 1; Figure S1). However, fuel amount seemed to be slightly more limiting, given that Emas National Park was the landscape with the highest fire frequency and higher MAP levels (but not the highest seasonality) (Figure 1; Figures S3 and S4). This interpretation is consistent with our field observations of increasing fuel amount from the low to the high fire landscape (Figure 5). In fact, regressing fire separately against MAP and RS indicates that

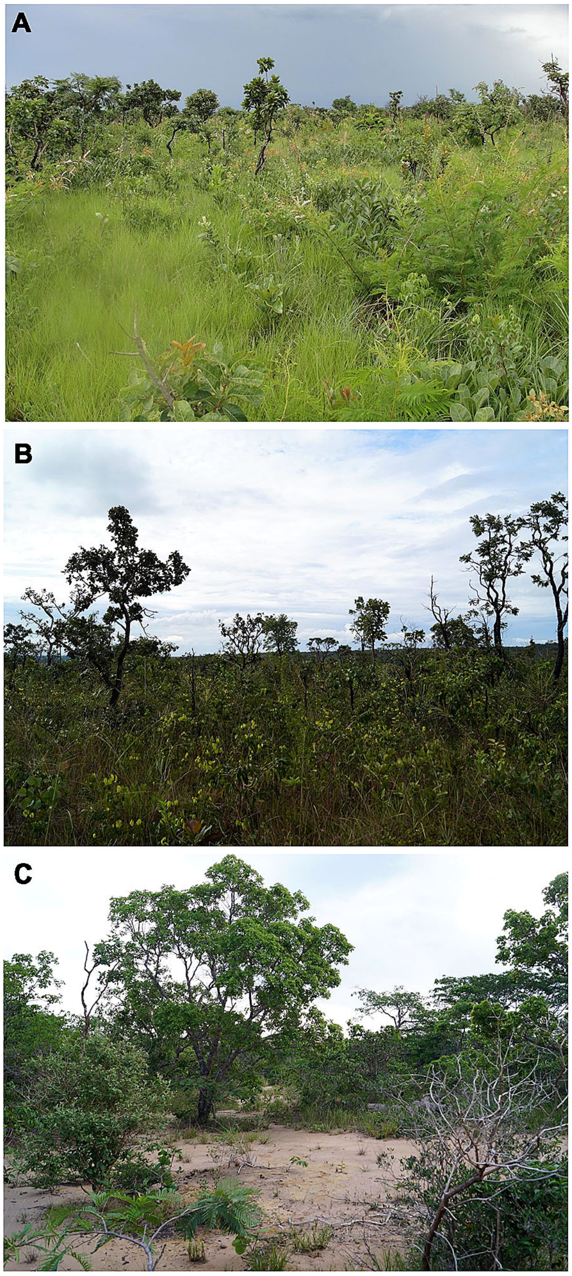

Figure 5. Examples of savannas in the high (**A**), mid (**B**), and low (**C**) landscapes. Note that the grass layer is tall and continuous in the high, also continuous in the mid, and patchy in the low. Photo credits: Vinicius L Dantas (**A**) and Paulo Bernardino (**B**, **C**).

the former explains more variability in fire than the latter (R^2_{adj} of 0.33 and 0.03, respectively). This is consistent with independent evidence showing that fire frequency declines with precipitation within the considered range (Figure S1; van der Werf and others 2008). Thus, while seasonality certainly plays a key role in defining the range of precipitation in which savannas occur, our results suggest that, in regions where the climate is already seasonal, the effect of moisture in increasing fuel loads seems to be more important (Pausas and Ribeiro 2013). At this scale, a large fraction of the variability in fire is also predicted to be explained by vegetation (Figure 4; Pausas and Dantas 2017).

The patterns shown here for the high and mid landscapes should not be confounded with a successional gradient. First, because bimodality in key ecosystem properties is a pattern characteristic of systems that present hysteresis and alternative states, not of successional gradients (Warman and Moles 2009). Second, because successional gradients do not show a threshold-like pattern in functional traits with increasing successional age (Lohbeck and others 2013; Boukili and Chazdon 2017). Finally, the direction of the functional changes from low to high woody cover shown here for traits like SLA and WD are opposite to what is generally observed in successional gradients (Lohbeck and others 2013; Boukili and Chazdon 2017). In fact, even in the low landscape, in which a threshold-like pattern was not observed for functional traits, the direction of the trait changes is not consistent with a successional gradient, suggesting an alternative explanation for this mosaic (for example, history, resource availability).

CONCLUSION

By integrating different spatial scales (that is, community and landscape), we showed that forest and savanna functional distinction and magnitude of functional change increase with fire activity (and potentially precipitation) for seasonally dry tropical ecosystems. Moreover, for the rainfall gradient evaluated in the Cerrado region, we found evidence that fire activity loses importance as we move from wetter to drier climates and from more seasonal to less seasonal precipitation regimes. Thus, we not only confirmed previous findings that savanna and forest occur as alternative stable states in the humid seasonal Neotropics (Dantas and others 2013, 2016), but also integrated these findings with broader spatial scales and potentially with climatic patterns. These results are consistent with theoretical predictions, as well as evidence from a range of spatial scales, and provide insights on the effects of different fire frequencies at the regional scale for a better understanding of how future changes in rainfall patterns and fire activity may shape biome distribution in the tropics.

ACKNOWLEDGEMENTS

The authors are grateful to the São Paulo Research Foundation (FAPESP; processes 2013/50169-1, 2014/06100-0, and 2014/06453-0) for the financial support and scholarships granted to the authors. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES)—Finance Code 001. M.H. is currently supported by a grant from Instituto Serrapilheira/Serra-1709-18983, R.O. by a Grant from FAPESP 19/07773-1, and J.P. by a Grant from the Spanish government (PGC2018-096569-B-I00). The authors are also grateful to the Tribes research group for intellectual and logistic support. To L. O. Anderson for helping with the satellite data and field campaign planning. To the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) for research permission; IBGE Ecological Reserve staff for all the assistance; A. I. Sosa, F. Piccolo, F. M. Seraphim, and P. Monteiro for helping with the fieldwork; G. Shimizu and D. Alvarenga for helping with species identification. The authors have no conflict of interest to declare.

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