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Key Points

- Spaceborne lidar from NASA’s ICESat-2 mission captures woody vegetation structure across the Cerrado biome of Brazil.
- Mean canopy heights decreased with increasing burn frequency, with the biggest declines observed for forests and savannas.
- Post-fire recovery of woody vegetation takes decades, with faster gains in canopy cover in forests than canopy heights.

Abstract

Fires mediate grass and tree competition and alter vegetation structure in savanna ecosystems, with important implications for regional carbon, water, and energy fluxes. However, direct observations of how fire frequency influences vegetation structure and post-fire recovery have been limited to small experimental field studies. Here, we combined lidar-derived canopy height and canopy cover from NASA’s Ice, Cloud and land Elevation Satellite-2 (ICESat-2) with over two decades of satellite-derived burned area data to provide the first biome-wide estimates of post-fire changes in canopy structure for major vegetation types in the Cerrado. Mean canopy height decreased with increasing burn frequency for all natural cover types, with the greatest decline observed for forests and savannas. The ability to separate changes in fractional canopy cover from height growth using lidar data highlighted the long time scales of vegetation recovery in forests and savannas after fire. For forests in medium and high precipitation areas, canopy cover returned to unburned values within five years following fire, whereas mean canopy height remained below unburned values, even in the oldest fires (14-20 years). Recovery was slower for savannas, with average values of both fractional cover and canopy height below unburned areas after 14-20 years, and recovery times increased with decreasing rainfall. Our results suggest only gradual increases in woody vegetation height and fractional cover over decades, even in mesic or wet savanna regions like the Cerrado. Infrequent fire

activity, particularly in areas with greater land management, influences ecosystem structure across the biome, with important consequences for biodiversity conservation.

Plain Language Summary

Savanna ecosystems are adapted to fire, and frequent burning maintains a mosaic of grass, shrub, and tree cover. Globally, fire activity in savannas has declined in recent decades with increasing fragmentation. This decline raises questions about the magnitude and duration of fire impacts on savanna vegetation and potential increases in woody cover in the absence of fire. We used satellite lidar, burned area, and land cover data to examine the influence of fire frequency and time since the last fire on the structure of vegetation in the Cerrado biome of Brazil. Our results show that the height and fractional cover of woody vegetation decline with increasing fire frequency in all Cerrado vegetation types. Regrowth of woody vegetation following fire is slow, even in the wettest Cerrado regions. Canopy cover returns to pre-burn values within five years in forest areas receiving medium and high precipitation but remains below unburned areas even after 14-20 years for savannas. Canopy height remains below pre-burn values for decades after fire in both forests and savannas. This slow rate of woody vegetation recovery following fire suggests that less frequent burning in the Cerrado may not lead to rapid increases in vegetation carbon stocks.

Introduction

Fires are an integral part in the Earth system, causing widespread changes in ecosystem structure and function, atmospheric chemistry, and climate (Bowman et al., 2009). Fire-induced changes in the horizontal and vertical structure of vegetation drive substantial shifts in ecosystem carbon storage, surface energy balance, and species' habitats (Frolking et al. 2009). Savannas and grasslands, which occupy about 20% of the land surface and store 15% of vegetation carbon stocks, account for almost 85% of the global annual burned area (Parr et al., 2014; Van der Werf et al., 2010). Fires have played an important role in the evolution of savannas and grasslands across the globe (Beerling & Osborne, 2006; Edwards et al., 2010; Van der Werf et al., 2010). Widespread changes in savanna fire regimes in response to human activity (Andela et al., 2017) and climate (Abatzoglou et al., 2019) therefore have the potential to alter vegetation structure and carbon storage in savanna ecosystems.

The Brazilian Cerrado (Figure 1a) is a large tropical savanna biome with high levels of biodiversity and endemism (Myers et al., 2000; Strassburg et al., 2017). The Cerrado biome includes a gradient of physiognomies from pure grasslands to open and closed-canopy woodlands and gallery forests (Coutinho, 1990). Cerrado vegetation is characterized by the presence of deep roots developed as a

response to long dry periods, fire, and extremely weathered soils (Morais et al., 2020). It is estimated that the below-ground biomass is twice as large as the aboveground biomass, leading some ecologists to describe the Cerrado as an “inverted forest”.

Fire is one of the factors that contributes to the structural heterogeneity of the Cerrado. As a mesic savanna, the Cerrado biome can support both savannas and forests as distinct and stable alternative states; fire regimes exert significant control over the proportion of grasses and tree cover, and therefore the distribution of open and closed-canopy formations (Staver et al., 2011; Touboul et al., 2018). At high frequencies, fires can reduce woody cover and promote the growth of grasses (Bond et al., 2005; Fidelis, 2020). On the other hand, fire suppression allows trees to encroach into grass-dominated landscapes, causing a decline in the shrub and herbaceous cover (Abreu et al., 2017; Vieira et al., 2018). Many savanna trees have specific adaptations to fire, including thick corky bark, resprouting ability, and a larger investment in below ground biomass (Archer et al., 1996; Coutinho, 1990; Felfili et al., 2000). Most herbaceous species in the Cerrado have underground meristems that favor quick recovery following surface fires—about 70-80% recovery of the herbaceous biomass within one year after fires in open savannas (Andrade, 1998; Klink et al., 2020) and a complete recovery after two years (Neto et al., 1998). Overall, forest species are less adapted to fires making them more sensitive to frequent burns (Hoffmann, 1996; Staver et al., 2020).

Contemporary Cerrado fire regimes are strongly influenced by land management. Since the 1980s, roughly 40% of the area under native Cerrado vegetation has been converted to croplands and pastures as part of the broader expansion of agricultural production in Brazil (Zalles et al., 2021). While fire is the primary tool for agricultural expansion in the Cerrado (Pivello, 2011), land use intensification and fragmentation have resulted in fire suppression in agricultural landscapes after the initial phase of land conversion (Rosan et al., 2019). By contrast, fires in remaining areas of native Cerrado vegetation are more frequent, particularly in seasonally flooded grasslands and savanna-dominated regions (Arruda et al., 2021). Variability in fire frequency as a function of land management and fragmentation may contribute to changes in vegetation structure and biodiversity across the biome.

Three-dimensional (3-D) vegetation structure can provide valuable information about the distribution and diversity of habitat conditions and the rates and mechanisms that contribute to vegetation recovery following disturbances, such as fire. Knowledge of the magnitude and duration of changes in Cerrado vegetation structure from fire is essential to accurately model regional carbon, water, and energy fluxes and design appropriate land-management strategies to sustain ecosystem services, including biodiversity. Several plot-based studies using prescribed burns suggest that recovery rates depend on the Cerrado vegetation type, and that fire frequency affects percent woody cover and above-ground nutrient concentrations (de Castro & Boone Kauffman 1998; Moreira, 2000; Oliveras et

al., 2012; Stradic et al., 2018). However, confirming these changes in vegetation structure in response to fire across the Cerrado biome requires other approaches. Satellite imagery from passive optical remote sensing platforms have been used to estimate trends in the fire frequency, intensity and burned area across the Cerrado (Araújo et al., 2012; Campagnolo et al., 2021; Mataveli et al., 2018; P. S. Silva et al., 2021) but these data do not directly capture structural changes in response to different fire regimes.

New satellite lidar data provide a broad sample of ecosystem structure across the Cerrado. (C. A. Silva et al., 2021) recently used lidar data from the Global Ecosystem Dynamics Investigation (GEDI) to assess aboveground biomass, an aggregate measure strongly correlated with vegetation structure. However, the large GEDI lidar footprint (25 m) makes it difficult to distinguish the contributions from trees, shrubs, and grass vegetation to the lidar waveform. By contrast, NASA’S ICESat-2 lidar provides information at the individual photon level that can inform our understanding of the vertical and horizontal heterogeneity in vegetation structure in the along-track direction. ICESat-2 data have been used to estimate canopy height and canopy cover (Yu et al., 2022), aboveground biomass (Narine et al., 2020; C. A. Silva et al., 2021), and burned area (Liu et al., 2020) for different ecosystems across the globe. The large and growing sample of global vegetation structure from ICESat-2 also enables studies of vegetation recovery following fire or other disturbances.

In this study, we combined canopy height and canopy cover information derived from ICESat-2 lidar data with over two decades of burned area data from the Moderate Resolution Imaging Spectroradiometer (MODIS) instruments on NASA’s Terra and Aqua satellites to provide the first biome-wide estimates of post-fire changes in canopy structure for the major vegetation types in the Cerrado. Our primary goals were to 1) quantify the influence of burn frequency on canopy height and canopy cover for the major Cerrado vegetation types and 2) estimate the canopy recovery as a function of time since fire. Based on the combination of contemporary lidar data and historic burn history information, we used a space-for-time sampling approach to investigate fire impacts on vegetation height and fractional canopy cover across the Cerrado biome. The magnitude of fire impacts on vegetation structure and the rate of canopy recovery are two important parameters that govern carbon accumulation in the Cerrado and the influence of changing fire regimes on the matrix of Cerrado cover types.

2. Data and Methodology

2.1. Land cover data

As part of the MapBiomass project, annual land use and land cover maps at Landsat 30 m spatial resolution were created for the period 1985-2020 for different biomes in Brazil (Souza et al., 2020). The accuracy of the MapBiomass land cover product for the Cerrado biome has been estimated to be around 80%, with spatial variability in native vegetation types and spectral similarity across

land cover classes cited as key factors that influence misclassification (Souza et al., 2020).

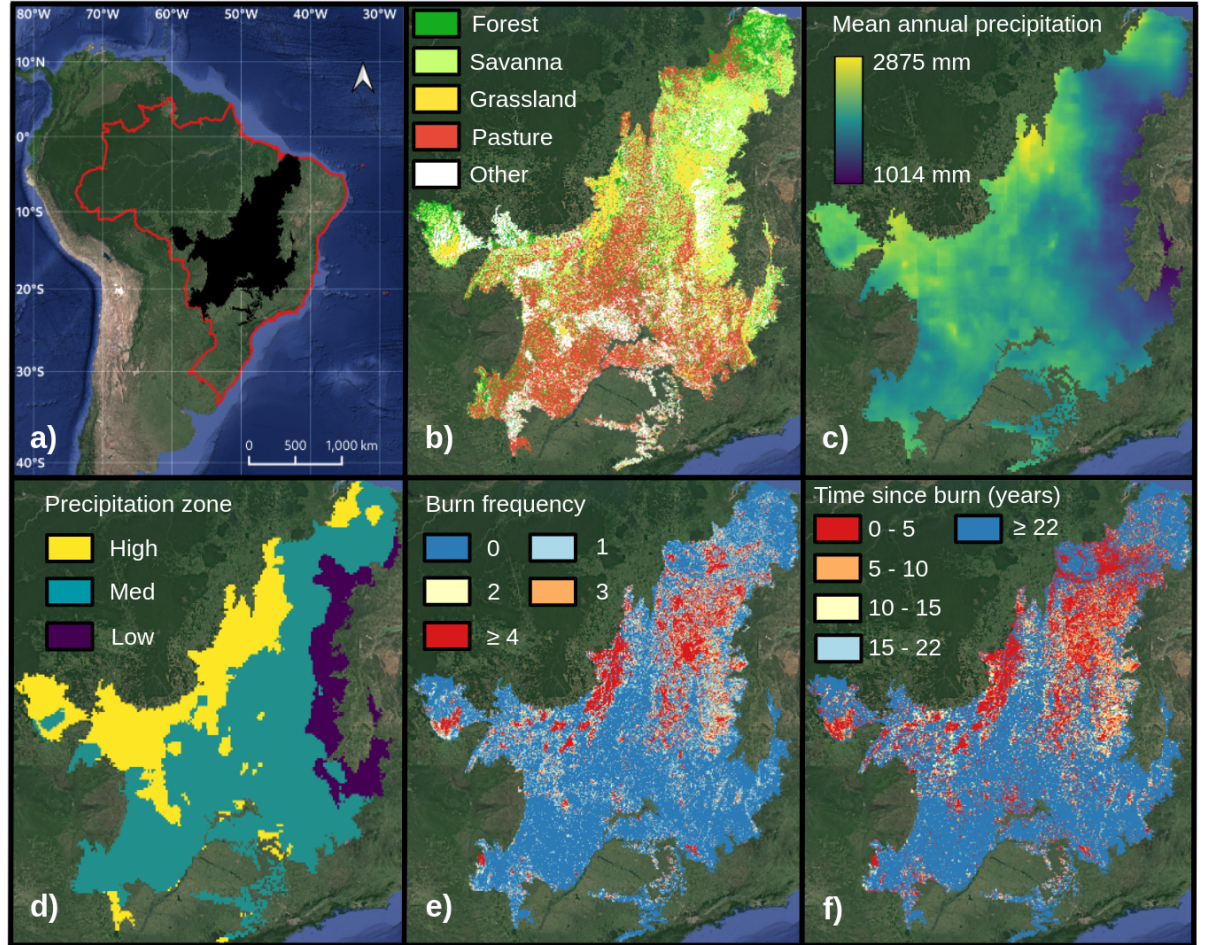


Figure 1: Cerrado vegetation structure is strongly affected by patterns of land use, precipitation, and fire regimes. **a)** The Cerrado (shown in black) is the second largest biome in Brazil (red outline). **b)** Major land cover types from the MapBiomas land cover product for the year 2019. **c)** The Cerrado is one of the wettest savanna biomes in the world, with mean annual precipitation (in mm) at 0.1° resolution ranging between 1014 - 2875 mm. **d)** The biome was divided into three precipitation zones (low, medium and high) based on percentiles of mean annual precipitation. MODIS burned area data at 500 m resolution over the period 2001-2021 show stark differences in **e)** burn frequency and **f)** time since fire (years) across the biome, with savanna and grasslands burning multiple times, whereas managed landscapes experienced little to no fire activity.

We used the collection 5 annual land cover maps for the Cerrado biome for the

years 2001 through 2020 from the MapBiomass data portal (MapBiomass 2020). Four Cerrado land cover types – pastures (occupying about 31% of the biome), savanna (29%), forest (14%), and grassland (8%), were considered in this study (Figure 1b). Other land cover classes, such as croplands (occupying roughly 15% of the biome), urban areas and water, were excluded.

Over the past several decades, the Cerrado has been a global hotspot of agricultural expansion, due in part to less stringent protection of native vegetation in the Cerrado compared to forested biomes in Brazil, including the Amazon (Strassburg et al., 2017). For our study, places experiencing frequent land cover transitions could pose a challenge in studying vegetation response to wildfires and recovery trajectories. Therefore, we included only those areas which did not experience any change in land cover over the period 2001-2020, representing about 76% of the biome-wide area under the four land cover types for which ICESat-2 data was available.

2.2. Precipitation data

Annual precipitation varies from 1014 to 2875 mm in the Cerrado, and this variability may contribute to differences in pre-fire vegetation structure and post-fire recovery. To capture the gradients in precipitation across the biome, we used the version 06 release of global monthly final run IMERG precipitation data (in mm) at 0.1° (10 km) resolution for the period Jan, 2001 through Dec, 2019 (Huffman et al., 2014). Datasets were clipped to the Cerrado biome extent and yearly precipitation sums were calculated for each 10 km pixel for the 19 years to generate an average annual precipitation map for the Cerrado biome (Figure 1c).

There is a clear east-west gradient in the annual precipitation across the Cerrado (Figure 1c), with the eastern region bordering the Caatinga receiving low average annual rainfall of about 1000-1500 mm, whereas the western region bordering Amazônia receives as much as 2200 to 2800 mm rainfall. The central part of the Cerrado receives a moderate amount of rainfall (1500 - 2200 mm). We created a categorical precipitation map using percentiles of the biome-wide precipitation distribution to delineate areas of low (0-20), moderate (20-80), and high (80-100) precipitation (Figure 1d).

2.3. Lidar data processing

ICESat-2, while developed primarily to measure ice sheet elevation and sea ice thickness, also provides a robust global sample of vegetation height and canopy structure (Malambo & Popescu, 2021; A. Neuenschwander et al., 2020; C. A. Silva et al., 2021). ICESat-2's photon-counting laser altimeter, the Advanced Topographic Laser Altimeter System (ATLAS), splits a single laser pulse into six profiling beams of green (532 nm) laser light (Neumann et al., 2019). These beams are arranged in 3 beam pairs, each containing a strong and a weak beam, with an energy ratio of 4:1. The ATLAS instrument operates at a high frequency of 10 kHz resulting in one laser pulse every 70 cm along the ground with a nominal footprint diameter <17 m (Neumann et al., 2019). ICESat-2 provides

robust estimates of heights, with a bias of ± 3.3 cm and better than ± 7.2 cm precision on the flat interior of Antarctic ice sheets (Brunt et al., 2021).

We utilized two standard ICESat-2 data products to estimate woody vegetation height and fractional cover across the Cerrado biome. We downloaded 1838 version 5 files from the National Snow and Ice Data Center (NSIDC) for the Land, Water, and Vegetation Elevation Product (ATL08, (A. L. Neuenschwander et al., 2021)) and the L2A Global Geolocated Photon Data Product (ATL03, (Neumann et al., 2021)) for ICESat-2 orbits with coverage of the Cerrado from September 28, 2018 through June 14, 2021. We extracted data for the three strong beams, and filtered data using ATL08 parameters to exclude 20-m segments with the presence of water, urban areas, clouds, and aerosols. Based on their position in the vertical profile, the ATL08 algorithm classifies each photon (ph) as either ground, canopy or top of the canopy and calculates their height (h in m) above the interpolated ground surface (ph_h). We derived the mean canopy height (in m) for each 20 m segment by calculating the average ph_h for all the canopy photons within that segment. For segments with no canopy photons, the mean canopy height was set as zero. We also calculated the percent canopy cover for each 20 m segment as the ratio of the number of canopy photons (including top of canopy photons) to the total number of photons in each segment. After applying the land cover mask, we utilized a total of 6.18 million ICESat-2 20 m segments, containing about 358 million photons, to characterize vegetation structure across the Cerrado biome. Data processing was performed using Python 3.7 (Van Rossum & Drake, 2009).

2.3. Satellite-derived burned area metrics

The Terra and Aqua combined MCD64A1 collection 6 burned area product (Giglio et al., 2018) is a 500 m global product which provides information about the day of year when the burn occurred. We used the collection 6 MCD64A1 data for the period January 2001 through June 2021 from the NASA LP DAAC portal (Giglio et al. 2015). Data were downloaded for the 5 tiles h12v10, h12v11, h13v09, h13v10 and h13v11, which collectively span the entire Cerrado biome. Image mosaics were created from the 5 tiles and pixels with high burn date uncertainty and data quality issues were excluded.

With the ICESat-2 data collected on different dates across the biome, burn frequency and time since burn were calculated such that they account for the date of the lidar data acquisition. For each 20-m segment, the burn frequency was calculated as the number of times the 500 m pixel containing the 20 m segment burned between Jan 2001 and the date when ICESat-2 data was collected. Similarly, time since burn was calculated as the number of years prior to the date of ICESat-2 data acquisition when the 500 m pixel containing the 20m segment burned. Burn frequency values were further binned into five classes: 0, 1, 2, 3, ≥ 4 , respectively.

3. Results

The highest frequency of fires occurs in the grassland and savanna-dominated

regions of the Cerrado, including the upper Araguaia River watershed bordering the Amazon and protected areas of native vegetation in the northern portion of the biome (Figure 1e). Approximately 64% of the Cerrado biome never burned during the MODIS record, whereas 13%, 7%, 5% and 11% burned 1, 2, 3 and greater than or equal to 4 times, respectively. There is a distinct north-south gradient in Cerrado fire activity, with two-thirds of the burned area concentrated in the northern region referred to as MATOPIBA, a territory defined by the extent of Cerrado vegetation in the states of Maranhão (MA), Tocantins (TO), Piauí (PI), and Bahia (BA). Managed cover types in the southern Cerrado, including pasture and croplands, experienced little or no fire activity in the past two decades. The spatial distributions of the time since last fire and fire frequency were similar (Figure 1f). About 19% of the biome burned in the last 5 years, with 9%, 6% and 2% of the biome experiencing fires 5-10 years, 10-15 years and 15-22 years ago, respectively.

Like fires, vegetation structure was strongly influenced by regional land management. The spatial distribution of mean canopy heights from ICESat-2 at 1 km resolution (Figure 2b) captures the biome-wide variations in woody vegetation structure, with tallest canopies in forest and savanna classes and shorter and less variable canopy cover in grassland and pasture cover types (Figure 2). Most 1 km grid cells contain at least 3200 20-m segments, and sampling density was generally high across the biome except in cloudier areas along the Amazon biome boundary (Figure 2a). Patterns of fractional canopy cover largely mirror those of canopy heights in forest and savanna cover types (Figure 2c), with > 70% canopy cover in forested areas. Land cover types with less woody vegetation stand out as contiguous areas with < 20% fractional canopy cover in grasslands, pastures, and cropland areas. Overall, ICESat-2 data confirm the structural differences among the forest and savanna classes and the gradient in woody cover across native vegetation types in the Cerrado (Figures 2d and 2e).

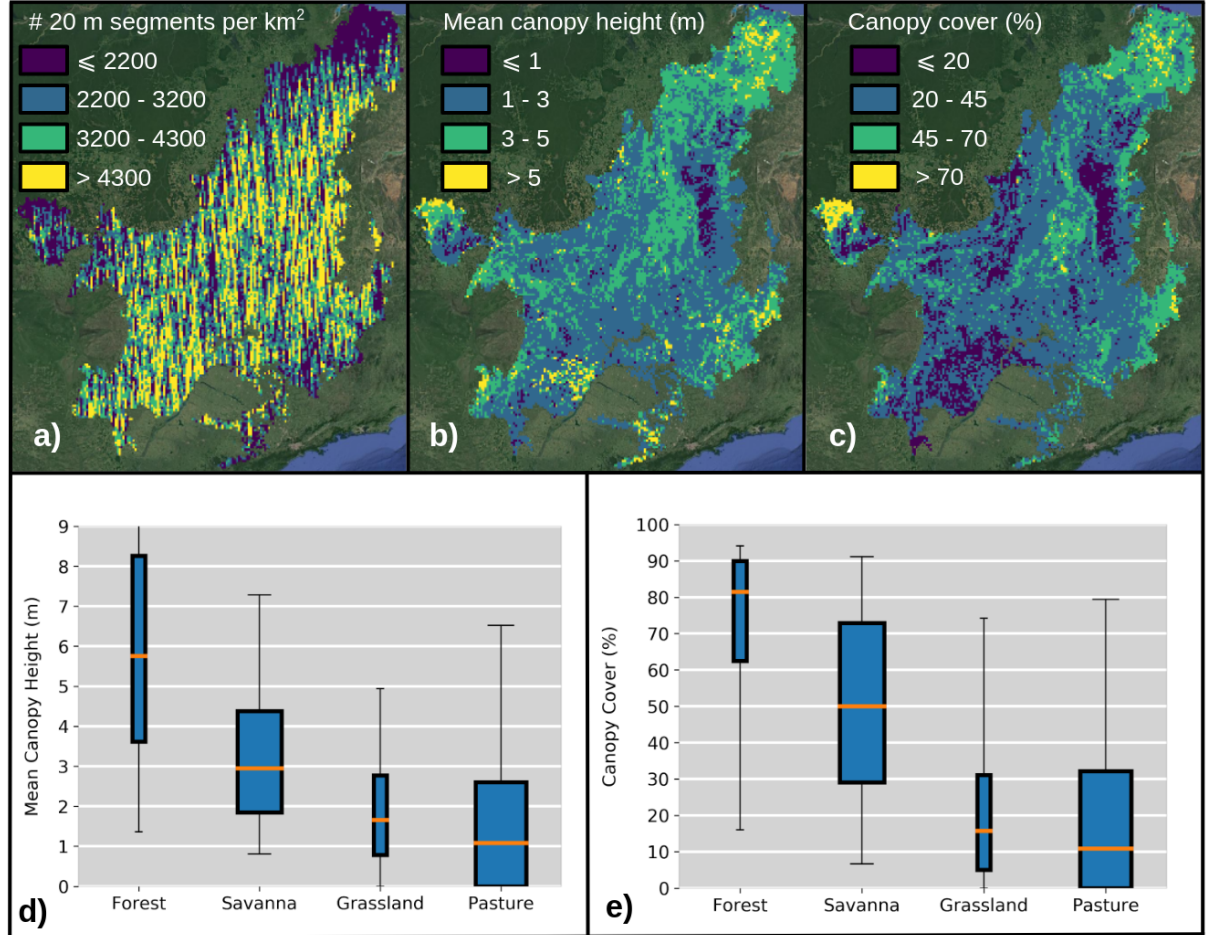


Figure 2: Estimated mean canopy heights and percent canopy cover derived from ICESat-2 lidar data capture differences in vegetation structure across the Cerrado. Spatial maps of **a)** the number of 20 m ICESat-2 segments **b)** mean canopy height (in m) based on lidar returns classified as canopy or top of canopy and **c)** percent canopy cover at 1 km resolution. **d)** Distribution of lidar-derived mean canopy heights (in m) for all 20-m segments in each land cover class and **e)** percent canopy cover for the major vegetation types. Widths of the boxplots are proportional to the number of 20 m segments in each class.

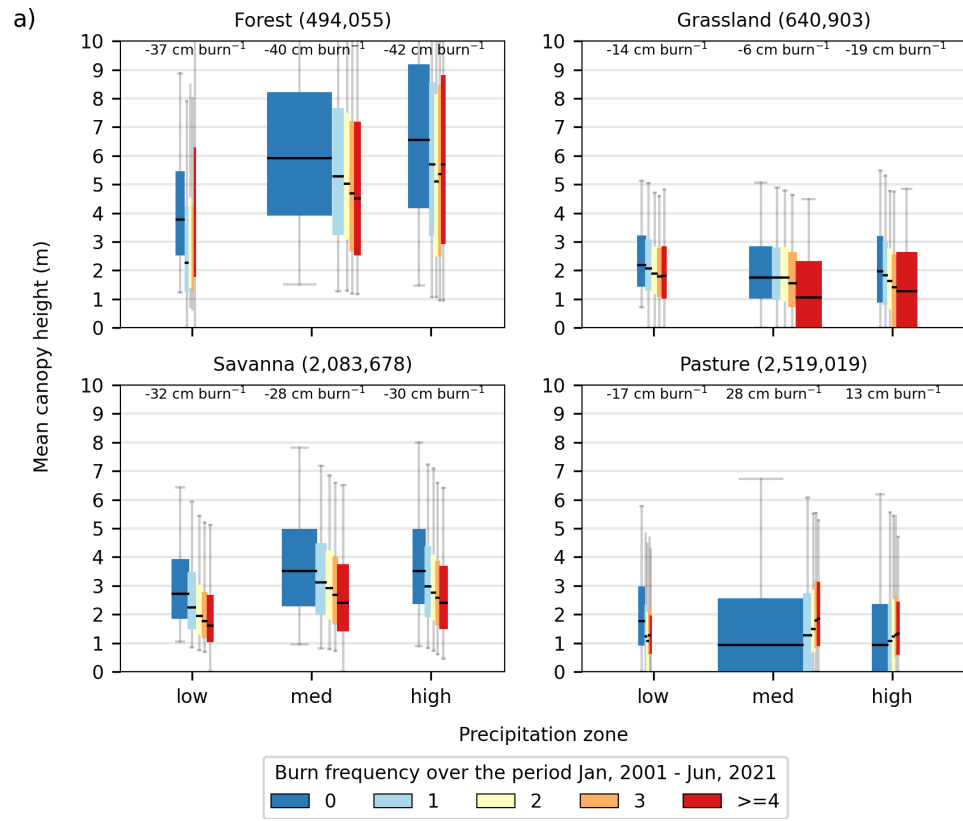
The distribution of canopy heights in grassland and pasture areas partly reflects the 50 cm threshold for canopy photons in the ATL08 algorithm (Figure 2, Figure S1). In herbaceous cover types, this vertical threshold leads to a classification of lidar returns from low vegetation as ground returns (Figure S2). Given that herbaceous vegetation averages 60 cm in the Cerrado (Ratter et al. 1997), the resulting height estimates from ICESat-2 are therefore strongly influenced by woody vegetation, rather than the mean height of vegetation including both

herbaceous and woody plants. Overall, ICESat-2 detected some fractional tree or shrub cover (> 50 cm) in about 81% and 70% of the 20 m segments in grasslands and pastures, respectively. The sensitivity to woody vegetation height and cover is a strength of ICESat-2 data for this study, where post-fire growth of woody plants drives observed changes in vegetation structure. Importantly, the distributions of mean canopy heights and fractional canopy cover were robust to differences in solar background noise during daytime observations (Figure S4), with mean canopy heights approximately 20 cm higher in daytime data, and seasonal changes in leaf area (Figure S5), with less than 10% differences in canopy cover between wet and dry seasons, primarily in savanna and grassland areas. We therefore used all ICESat-2 strong beam data for our analysis of fire impacts on vegetation height and cover (Table S1).

Canopy height and fractional cover varied with fire frequency across land cover types and precipitation zones (Figure 3, Figure S6). The decline in mean canopy height averaged 40 cm per fire in forests and 30 cm per fire in savannas. The mean height loss in response to increasing fire frequency was consistent across precipitation zones within forests and savannas.

Changes in the mean canopy height of woody vegetation in grassland and pasture areas with increasing fire frequency were more variable (Figure 3a). In grasslands, the mean height of woody vegetation declined with increasing fire activity in the low and high precipitation zones, but vegetation heights in the moderate precipitation zone only declined in cases with three or more fires. Pasture areas showed the opposite trend, with increasing mean height of woody vegetation with increasing fire frequency. Given the role of fire in the land cover conversion process, it is possible that this pattern reflects the more frequent use of fire to clear and manage pasture lands in areas with higher initial tree cover.

The response of canopy cover to increasing fire frequency was somewhat different than canopy height (Figure 3b). In forests, increasing fire frequency had a limited impact on fractional canopy cover, especially in regions with moderate precipitation ($<1\%$ loss per fire). This more muted response may reflect differences in time since fire, and a more rapid recovery of canopy cover following disturbance than height growth of surviving woody



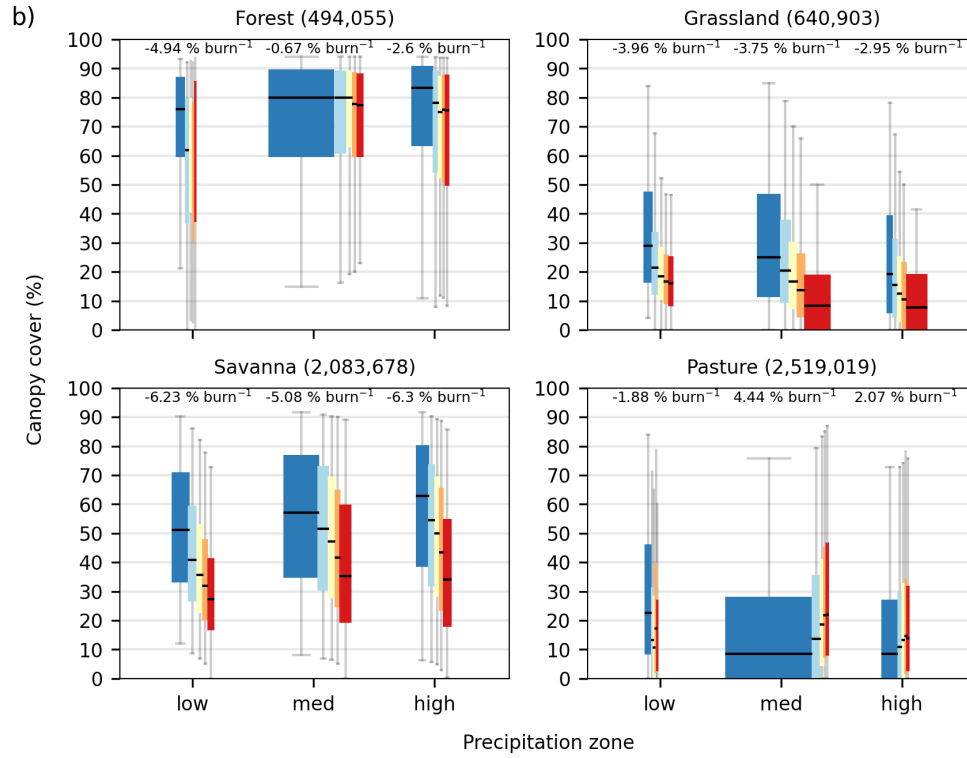


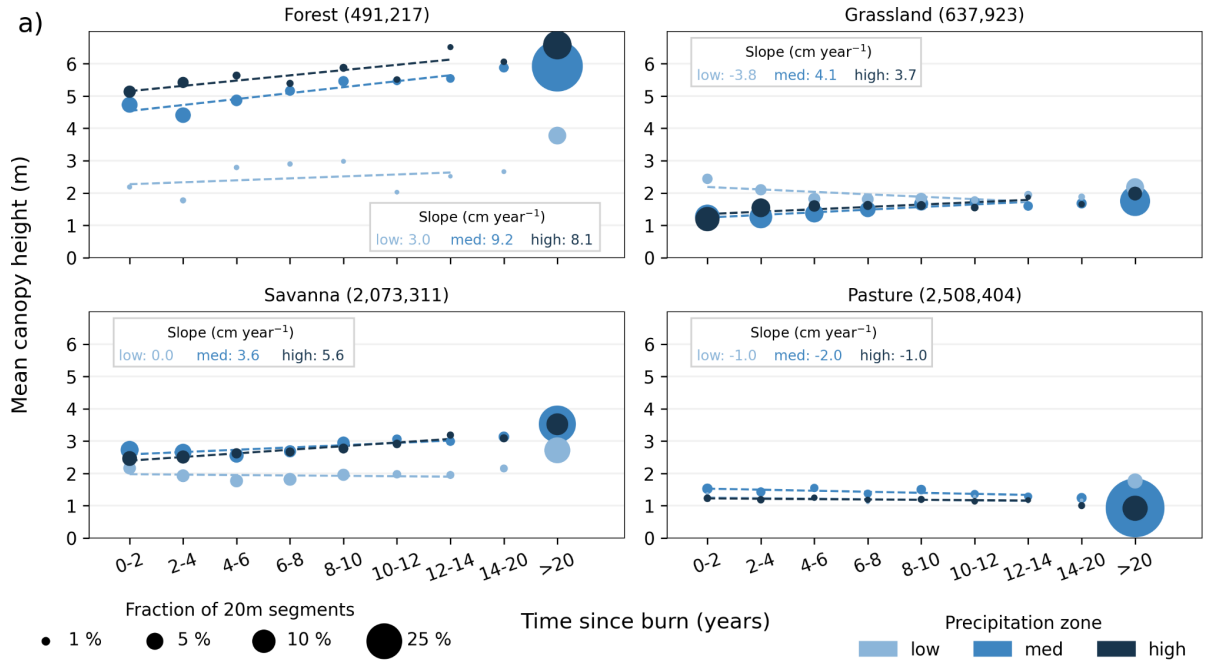
Figure 3: a) Mean canopy heights (in m) and **b)** canopy cover (%) decreased with increasing burn frequency for all natural cover types across all precipitation zones. Figures in brackets represent the number of 20m segments over each land cover type. The width of each individual box plot is proportional to the number of segments available for a given land cover type and precipitation zone. Numbers at the top of each subplot represent the slope of the line of best fit through the medians of the boxplots for the burn frequency classes 0,1,2 and 3 for each precipitation zone.

vegetation. In savannas, increasing fire frequency led to a strong and consistent decline in fractional canopy cover of 5.1-6.3% per fire across all precipitation zones. In contrast to changes in woody vegetation height in grasslands, the fractional cover of woody vegetation declined 3-4% per fire in grasslands across all precipitation zones. In pastures, the fractional woody cover increased with fire frequency in the moderate and high precipitation zones, similar to patterns of mean height in woody vegetation in these managed areas.

Precipitation has a substantial impact on the canopy height recovery for forests, savannas, and grasslands (Figure 4a), with higher recovery rates in areas receiving > 1500 mm rainfall. Mean canopy heights in forests increased by 8.1 cm year⁻¹ and 9.2 cm year⁻¹ in high and medium precipitation areas, compared to 3 cm year⁻¹ in areas receiving < 1500 mm annual rainfall. Compared to

forests, canopy height gains in savanna and grasslands were smaller. While canopy height recovery continued for over 20 years after fires, recovery of fractional cover was more rapid (Figure 4b), especially for forests in medium and high precipitation zones, with a return to levels in unburned vegetation within about four to six years after a fire event. For savannas, canopy cover increased by $1.1\% \text{ year}^{-1}$ and $1.8\% \text{ year}^{-1}$ in high and medium precipitation zones, respectively, compared to $0.7\% \text{ year}^{-1}$ in places receiving low rainfall. There was little change in canopy heights or fractional cover following fires in pastures across all precipitation zones. Recovery trajectories were robust to differences in solar background noise during daytime observations and the impact of seasonality on canopy cover (Figure S7).

Maps of the rate of recovery in savanna height and fractional cover capture spatial variability in ecosystem recovery following fire (Figure 5). Strong east-west patterns in the rates of recovery confirm the influence of precipitation on height gains (Pearson's $r = 0.35$) and increases in fractional woody cover (Pearson's $r = 0.44$) in savanna vegetation following fire. ICESat-2 data capture the spatial heterogeneity in ecosystem recovery, with three to four-fold differences in the rates of canopy height and fractional cover change following fire, even within a single land cover type.



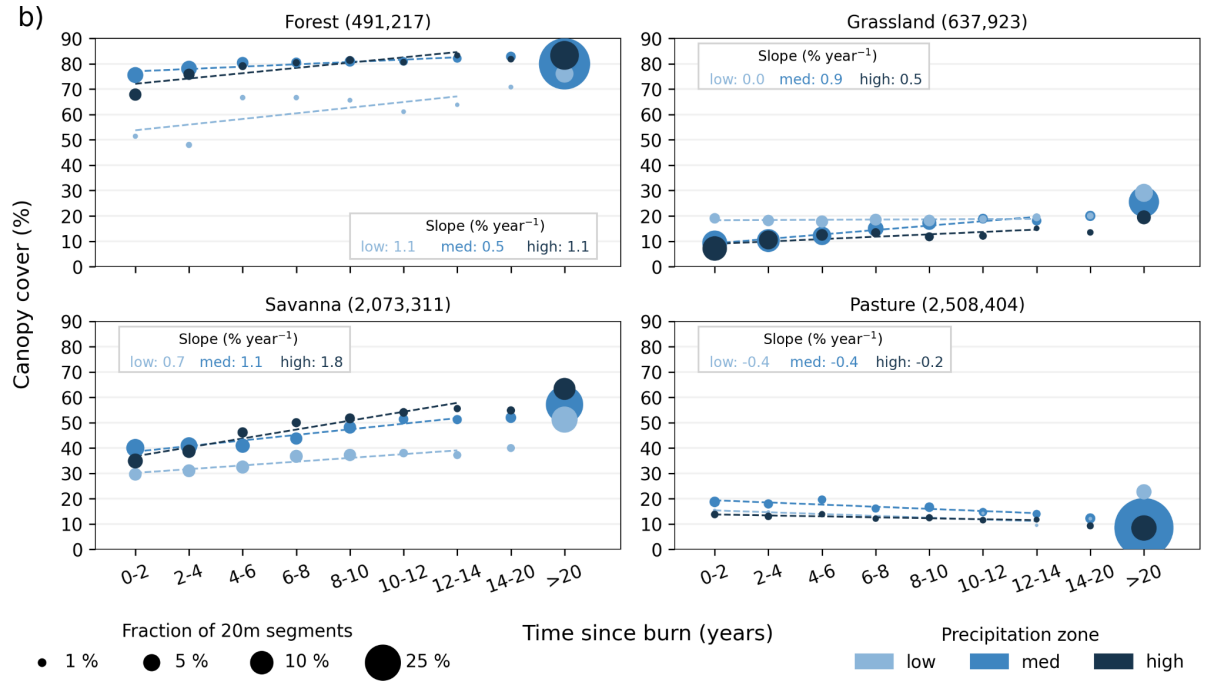


Figure 4: Recovery of a) canopy heights and b) fractional cover is generally quicker for forests, savanna and grasslands in areas receiving > 1500 mm annual rainfall. While canopy heights continue to recover for > 20 years post fires, recovery of fractional cover is much faster, especially for forests in medium and high precipitation zones which achieve a steady cover value in about four to six years. Each point represents the median value of the canopy height (or fractional cover) distribution with the size of the point proportional to the number of 20-m segments in that precipitation zone and time interval. Point sizes were normalized for each land cover type separately.

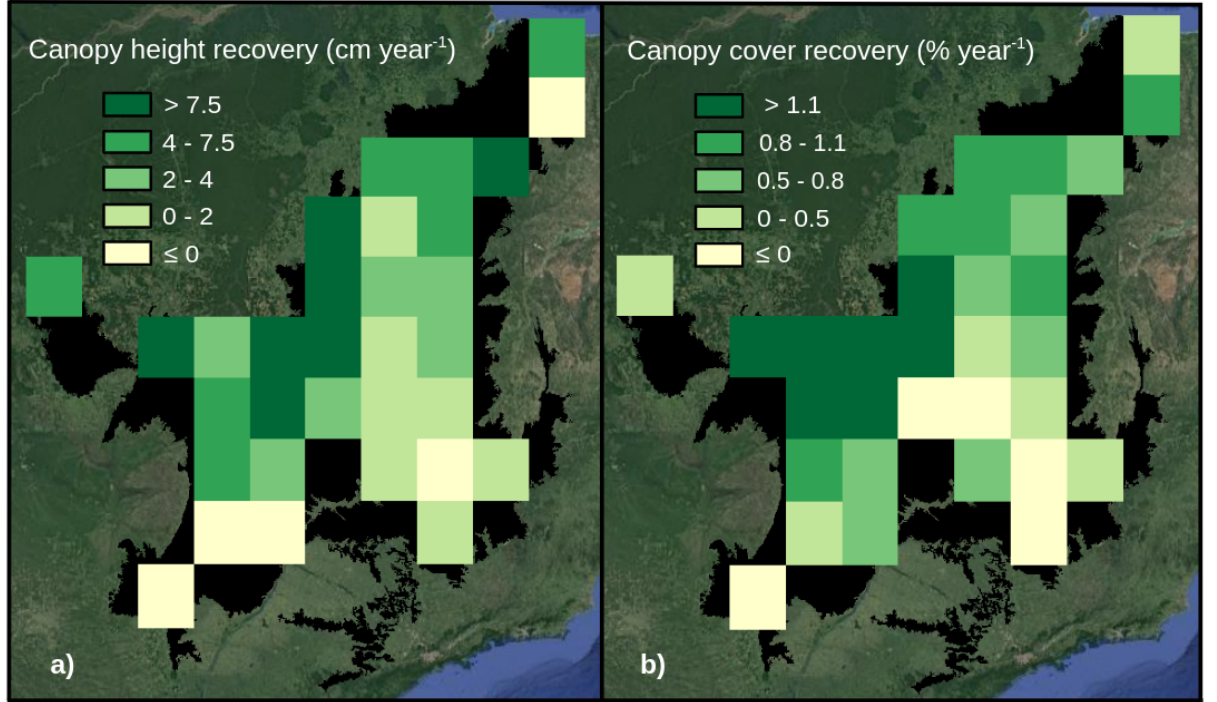


Figure 5: Spatial maps of **a)** canopy height and **b)** canopy cover recovery for Savannas at 2° resolution shows a clear east-west gradient, with higher recovery values in areas receiving more rainfall. For each 2° pixel, 20 m segments over the savanna were grouped into four time-since-burn classes - 0-5 years, 5-10 years, 10-15 years and 15-20 years. Canopy height recovery for each 2° pixel was defined as the slope of the line fitted through the median canopy height for each time-since-fire class. Recovery values were calculated for only those 2° pixels, which have at least 100 segments in each time-since-burn class.

4. Discussion

ICESat-2 lidar data capture subtle but important differences in the height and density of woody vegetation across the Cerrado biome in response to fire frequency and time since fire. The biome-wide sample from ICESat-2 expands upon our understanding of the influence of fire frequency on vegetation structure from field studies and experimental plots. Specifically, the ICESat-2 data cover a range of contemporary fire regimes, including both frequent and infrequent fire activity during the MODIS era. This large sample of vegetation structure confirms two important findings. First, the recovery of woody vegetation following fire is slower than expected from field studies, especially in savannas and grasslands. Second, fire frequency and time since last fire had a stronger impact on canopy height and fractional cover in areas with <1500 mm of annual precipitation than in wetter Cerrado environments. Together, these findings underscore the need to track changes in 3-D vegetation structure to

understand the diversity of habitat conditions across the Cerrado biome and the influence of fire disturbances on changes in woody cover.

Lidar-derived measures of 3-D structure suggest that post-fire recovery of woody vegetation in the Cerrado is slower than expected for one of the wettest savanna biomes (Lehmann et al., 2011). To our knowledge, this is the first study to use spaceborne lidar data to track biome-wide changes in vegetation structure following fires across the Cerrado, and our results provide important context for plot-level observations. Four factors may explain the differences between our study and previous work at the plot scale. First, experimental studies typically impose a high-frequency fire regime of annual to triennial burning (Higgins et al., 2007; Zhou et al., 2022), whereas these fire frequencies are uncommon at the biome scale during the 20+ years of MODIS observations. In addition, wildfires may differ from experimental fires (Beckett et al., 2022; de Castro & Boone Kauffman 1998; de Souza Aguiar, 2004; Kauffman et al., 1994) that are typically set under controlled conditions over small areas. Second, our study focuses more on the woody vegetation structure whereas field studies have often focused on herbaceous layer, where recovery rates are faster (Andrade, 1998; Klink et al., 2020; Neto et al., 1998). Third, performing a biome-wide analysis also captured the impact of precipitation on the vegetation response to fires. Precipitation mediates changes in canopy cover in response to fires and alters the rates of recovery of canopy heights and cover following fires. Post-fire recovery in more arid systems was longer compared to more productive systems (Figure 4), pointing to the role of total rainfall total on the rate of ecosystem recovery. It is possible that this reflects the importance of burn severity (Goetz et al., 2010; Karna et al., 2020), with higher severity and combustion completeness expected in drier areas and towards the end of the dry season (Levick et al., 2019; Ramos-Neto & Pivello, 2000). Fourth, experimental work has also considered the influence of seasonal timing on fire impacts (Smit et al., 2010; Veenendaal et al., 2018), a factor that we did not consider here, although most burned area in the Cerrado occurs in the mid to late dry season, a period often underrepresented in experimental work given the higher likelihood of fires escaping into neighboring areas (Vernooij et al., 2021).

Our results suggest that canopy height and percent cover decline with increasing fire frequency for all natural vegetation classes. This is consistent with results from plot-level studies which show that fire-driven losses in soil carbon and nitrogen content can have a strong effect on the tree community structure (Moreira, 2000; Pellegrini et al., 2018, 2021) and result in a transition to more grass-dominated landscapes (Beckett et al., 2022; Staver et al., 2011). Canopy height loss in forests and woody savannas was greatest after the first fire, potentially due to the loss of fire-intolerant species (Beckett et al., 2022; Staver et al., 2020), with decreasing height losses from successive fire events. Interestingly, changes in canopy cover as a function of burn frequency was larger for savannas than forests. However, the initial reduction in canopy cover following fire in forested areas (see Figure 3b) could be underestimated as a result of faster recovery rates and time since fire. In addition, fires of low- to moderate-severity

are known to be less damaging to canopy cover (Goetz et al., 2010; Karna et al., 2020). Given the moderate resolution of the burned area data in this study (500 m), variability in burn extent or severity within a larger fire perimeter may also confound estimates of fire impacts, especially for gallery forests or other wet microsites.

Our results indicate that canopy heights exhibit a gradual recovery following fire that plays out over decades, suggesting that there is a greater sensitivity of canopy vertical structure to fires than leaf area or fractional cover. This has consequences for many savannas that have seen declining fire frequencies over the past decades (Andela et al., 2017). Such long recovery time scales have also been reported by some plot-based studies (Gomes et al., 2014; Machida et al., 2021), which have shown that plant density values take decades to return to pre-burn levels. These results support insights from a study in South Africa (Zhou et al., 2022) which suggests a limited increase in the ecosystem carbon stocks due to long-term fire exclusion. While heights continue to recover over the entire MODIS record, canopy cover returned to pre-burn values within about five years for forests in medium and high precipitation zones. For savannas, fractional cover increases for 10-12 years post fire, after which point it stabilizes, even in the absence of fire activity. Differences in the recovery of canopy height and fractional cover highlight the importance of lidar data in tracking changes in vegetation structure. By contrast, passive optical data are primarily sensitive to fractional cover (Staver et al., 2011), and this limitation could potentially lead to overestimation of ecosystem recovery (Potapov et al., 2021). The results of this study also provide important benchmarks for the rates of woody cover change following fire for ecosystem models and our understanding of the influence of changing fire frequency on the land carbon sink (Bond et al., 2005; Fidelis, 2020; Rabin et al., 2017; Wu et al., 2022).

Managed and unmanaged Cerrado landscapes show stark differences in fire regimes, with pasture- and cropland-dominated areas in the southern Cerrado experiencing little to no fires compared to more frequent fires in natural vegetation in the northern Cerrado over the MODIS record (Mataveli et al., 2018; Rosan et al., 2019; P. S. Silva et al., 2021). The resulting mosaic of land cover types could also lead to smaller fires, making them harder to detect using coarse resolution satellite data (Pereira et al., 2017; Roteta et al., 2019; Santos et al., 2020). Compared to natural vegetation classes, pastures showed a muted response in terms of the recovery of woody vegetation following fires and overall changes in ecosystem structure. Farmers use fires as a management tool for land clearing, crop residue burning and pasture renewal (Pivello, 2011), and this management approach may partially explain why pasture lands with greater canopy heights and percent cover are associated with higher burn frequency.

Novel information from spaceborne lidar can help clarify long-standing questions regarding the impact of fires on tropical ecosystem function. ICESat-2 data are particularly valuable for identification of woody vegetation. Maps of canopy height revealed the presence of residual tall vegetation on pastures and cropland

areas that have low fractional canopy cover. This difference reflects the fact that the average canopy height only considers canopy returns, while the calculation of fractional canopy cover includes both canopy and ground photons. From a conservation perspective, our results therefore highlight the importance of landscapes with land use for ecosystem services (Foley et al., 2005), in addition to remaining areas of natural vegetation cover. By contrast, the low density of returns from ATLAS (based on both green laser energy and the photon-counting detectors) limits the ability to separate lidar returns from ground and herbaceous vegetation, although this issue is not unique to ICESat-2 (da Costa et al., 2021; Hopkinson et al., 2004; Streutker & Glenn, 2006). In this study, the ICESat-2 ground-detection algorithm (A. Neuenschwander & Pitts, 2019) likely masks the contribution from the herbaceous layer or woody fraction below 50 cm (see Figures S1, S2 and S3). Future collection of repeat track ICESat-2 data may increase the lidar sampling density and permit the separation of ground and low vegetation. In addition, these repeat measurements will offer an opportunity to verify the results from the space-for-time approach in this study for the direct losses of canopy height and fractional cover from fire. Finally, our results support ongoing work to understand the influence of changing fire regimes on savanna and grassland vegetation structure, including potential impacts on the land carbon sink (Andela et al., 2017; Wu et al., 2022; Zhou et al., 2022), and the potential to manage fire activities to reduce greenhouse gas emissions (Vernooij et al., 2021) and the risk of catastrophic fires in the future. The global extent of ICESat-2 data collection also facilitates the extension of this work to other savanna ecosystems to investigate changes in woody cover in response to climate and land use.

5. Conclusions

This study used spaceborne lidar and time series of satellite-derived burned area to study biome-wide patterns in fire response and recovery for Cerrado vegetation types. ICESat-2 derived canopy heights and percent cover capture the biome-wide variability in canopy structure of both managed and natural vegetation types. Our results highlight the importance of mapping canopy heights in addition to fractional cover, with striking differences in observed ecosystem impacts and recovery times following fire. While canopy heights continue to recover even after 14-20 years post fire for forests and savanna, recovery in fractional cover is much faster for forests in medium and high precipitation areas. Interestingly, while precipitation played an important role in the canopy height and cover recovery for forests and savannas, ecosystem impacts following fire were similar across the rainfall gradient. Consequently, ecosystem recovery to pre-fire levels was slower in more arid systems. Overall, the fire response and recovery were fairly subdued for managed landscapes, such as pastures, pointing to the growing influence of human activity across the Cerrado. These results could help improve our understanding of the carbon dynamics and ecosystem response to fires in tropical savanna biomes. Insights from this study could also help shape appropriate fire policies and conservation measures for the Cerrado.

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Open Research

All datasets used in this study are freely available. ATL03 (Neumann et al., 2021) and ATL08 (A. L. Neuenschwander et al., 2021) ICESat-2 data are available on the NSIDC data portal. Cerrado land cover maps can be downloaded in GeoTiff format from the MapBiomass data portal (MapBiomass 2020). Precipitation data at 0.1° resolution was downloaded from the IMERG data portal (Huffman et al., 2014). Collection 6 MCD64A1 burned area maps can be downloaded from the NASA LPDAAC portal (Giglio et al., 2015).

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