Rapid response of habitat structure and aboveground carbon storage to altered fire regimes in tropical savanna

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Abstract. Fire regimes across the globe have been altered through changes in land-use, land management and climate conditions. Understanding how these modified fire regimes impact vegetation structure and dynamics is essential for informed biodiversity conservation and carbon management in savanna ecosystems. We used a long-term fire experiment at the Territory Wildlife Park (TWP), northern Australia, to investigate the consequences of altered fire regimes for habitat structure and

5 aboveground carbon storage. We mapped vegetation three-dimensional (3D) structure in high spatial resolution with airborne LiDAR, across 18 replicated 1 ha plots of varying fire frequency and season treatments. We used LiDAR-derived canopy height and cover metrics to extrapolate field-based measures of woody biomass to the full extent of the experimental site ($R^2 = 0.82$, RMSE = 7.35 t C ha^{-1}), and analysed differences in aboveground carbon storage and 3D structure among treatments. Woody canopy cover and biomass were highest in the absence of fire (76 % and 39.8 t C ha^{-1}) and lowest in plots burnt late in the

10 dry season on a biennial basis (42 % and 18.2 t C ha^{-1}). Woody canopy vertical profiles differed among all six fire treatments, with greatest divergence in height classes < 5m. Our results highlight the large extent to which fire management can shape 3D structural patterns in savanna landscapes, even over time frames as short as a decade. The structural profile changes shown here, and the quantification of carbon reduction under late dry season burning, have important implications for faunal habitat conservation and carbon sequestration/emission reduction initiatives in the region.

15 ## 1   Introduction

Fire is an integral component of the functioning of savanna ecosystems, exerting top-down control on woody vegetation structure (Bond and Keeley, 2005; Sankaran et al., 2005). Savanna fires restrict vegetation vertical growth through a 'fire-trap' mechanism, whereby young trees are constrained to low woody resprouts under high fire frequencies (Higgins et al., 2000; Freeman et al., 2017). A lengthening of the fire-free interval allows trapped woody plants to grow above flame height, en-

20 abling them to reach mid- and upper canopy heights, with long-term consequences for size-class distribution and structural heterogeneity (Helm and Witkowski, 2012; Levick et al., 2015a).

Three-dimensional (3D) heterogeneity of vegetation has long been valued as a key factor promoting faunal diversity through increased niche diversity (MacArthur and MacArthur, 1961; MacArthur, 1964). The structural modifications that fires impart on

savanna vegetation have been shown to impact both vertebrate (Woinarski et al., 2004) and invertebrate (Andersen et al., 2012) taxa. Fire-driven structural changes in savanna vegetation also have important implications for climate regulation, as savanna fires contribute significantly to atmospheric emissions of greenhouse gases through biomass combustion (Hurst et al., 1994; van der Werf et al., 2010). Despite the importance of quantifying fire induced changes to 3D structure in savanna vegetation,

5 current understanding of magnitudes and spatial patterns remains limited, and savanna fires represent large uncertainty in global vegetation models (Higgins et al., 2007; Scheiter et al., 2013). Gaining better understanding of how different fire regimes impact savanna vegetation structure is becoming increasingly urgent in the face of changing climate and land-management conditions that are triggering variations in the timing, frequency, intensity and duration of fires in the tropical biome (Alencar et al., 2015).

Fire frequency in Australian savannas is particularly high, with many regions burning twice in every three years on average

10 (Beringer et al., 2014). Many of these fires occur late in the dry season, producing high intensity burns that result in simplified vegetation structure (Bowman et al., 1988; Lehmann et al., 2009; Ondei et al., 2017). There are widespread concerns that such fire regimes are linked to dramatic declines in faunal populations, through the removal of ground layer vegetation (Lawes et al., 2015; Legge et al., 2015; Woinarski et al., 2015). Methane and nitrous oxide emissions from savanna fires are included in Australia's national greenhouse-gas accounts, and are responsible for approximately 3% of total accountable greenhouse-

15 gas emissions (Meyer et al., 2012). There is considerable interest in reducing the frequency and intensity of fires in northern Australia through strategic early dry season (April to July) burning, in order to reduce both greenhouse gas emissions and biodiversity decline (Russell-Smith et al., 2013). As such, the Australian Government has implemented legislation enabling landowners to claim carbon credits for reducing greenhouse gas emissions from savanna fires through early dry season burning (Carbon Farming Initiative - Emissions Abatement through Savanna Fire Management Methodology Determination 2015,

20 Department of Environment and Energy). Such changes to fire regimes in northern Australia are also likely to increase carbon sequestration in the landscape (Murphy et al., 2010; Richards et al., 2012), although there is currently no approved methodology for incorporating this into the national accounts.

An understanding of how different fire regimes impact habitat structure and carbon dynamics in tropical savannas is best achieved through detailed 3D measurements of vegetation structure at sites subject to long-term, replicated experimental fire

25 treatments. Traditional field-based inventory techniques are limited in their ability to quantify 3D structure, but light-detection and ranging (LiDAR) can now achieve this with high accuracy and precision in a repeatable and transferable manner (Lefsky et al., 2002; Levick and Rogers, 2008). Airborne LiDAR has a proven record in providing detailed 3D representations of savanna vegetation structure across time and space (Smit et al., 2010; Levick et al., 2012, 2015b), but has yet to be used for assessing vegetation biomass and structural diversity responses to experimental fires in savannas.

30 Northern Australia has a long history of savanna fire experiments (Williams et al., 2003), including the ongoing 'Burning for Biodiversity' experiment at the Territory Wildlife Park that has applied six fire treatments in three replicated blocks since 2004 (Scott et al., 2010). Here we integrate field-based measurements with airborne LiDAR to determine how variation in fire frequency and season affects the 3D habitat structure and aboveground carbon storage of woody vegetation. Our specific aims are to explore: i) if fire induced changes in woody vegetation structure and biomass are reliably detected by airborne LiDAR;

Table 1. Fire regime characteristics of the Territory Wildlife Park experimental site. Data are for the period 2004-2013

Treatment	Season	Frequency (yrs)	Intensity (kW m^{-1})	Times burnt
E1	June	1	589	9
E2	June	2	929	4
E3	June	3	424	3
E5	June	5	295	2
L2	October	2	1644	5
U	n/a	0	0	0

ii) how vegetation structural diversity and carbon storage respond to increasing fire frequency; and iii) the structural impact of higher-intensity, late-season fires compared to early-season fires.

2 Methods

2.1 Study site and experimental design

5 The Territory Wildlife Park is located 40 km south of Darwin in Australia's Northern Territory (Figure 1). The vegetation at the site is a mixed open forest and woodland savanna dominated by *Eucalyptus miniata* A.Cunn. ex Shauer, *Eucalyptus tetrodonta* F.Muell. and *Corymbia bleeseri* (Blakely) K.D.Hill and L.A.S. Johnson, with a grassy understory dominated by *Pseudopogonatherum contortum* (Brongn.) A.Camus, *Sarga intrans* F.Muell. ex Benth. and *Eriachne triseta* Nees ex Steud (Scott et al., 2010) . The soils are relatively shallow (0.5 to 1 m deep) gravelly red earths (Petroferric Red Kandosol) (Isbell, 10 2002) of the Kay land system within the Koolpinyah land surface group, and have developed predominantly from deeply weathered sandstones, siltstones and shales (Wood et al., 1985). The climate is wet-dry tropical with greater than 90% of annual rainfall (mean 1401 mm) falling in the wet season from November to April, and mean monthly maximum and minimum temperatures between 33.1 °C and 20.9 °C (Bureau of Meteorology, Commonwealth of Australia).

The fire experiment consists of 18 1-ha plots grouped into 3 blocks (A, B, C) arranged along a north-south transect (Figure 15 1). Soil depth increases from north to south, and the C blocks have higher soil moisture given their proximity to a small creek line. Six fire treatments were randomly assigned to each block: unburnt plots and plots burnt at fire return intervals of 1 (E1), 2 (E2), 3 (E3) and 5 (E5) years in the early dry season (June) and plots burnt every 2 years (L2) in the late dry season (Table 1). Prior to implementation of the burning treatments in 2004, all areas had been unburnt for at least 14 years when fire records started (except for a fire in 1992 and again in 2000 in the A blocks only).

Figure 1. Location and experimental design of the Territory Wildlife Park fire manipulation experiment.

2.1.1   Field-based estimation of above ground woody biomass

In each of the 18 plots, two 30 x 30 m subplots were established at the north-west and south-east corners, at least 10 m away from plot edges. In each subplot the species identity, location, height and diameter of all woody plants >2 m in height was recorded. The location of each individual plant was recorded to 0.3 m accuracy using a differential GPS with post-
5   processing (Trimble Inc.). Tree heights were recorded with a standard height pole (plants <8 m) or clinometer (plants >8 m), and stem diameter was recorded at 1.3 m with a diameter tape for all woody species except for the multi-stemmed shrubs *Calytrix exstipulata* and *Exocarpus latifolius*, in which case diameter was recorded at the stem base (0.1 m above the ground). Aboveground biomass was calculated for each individual tree using the equation developed by (Williams et al., 2005):

$$lnABG = -2.0596 + 2.1561(lnD) + 0.1362(lnH)^2 \tag{1}$$

10   whereby AGB = aboveground biomass (kg), D = stem diameter (m), and H = tree height (m). Individual tree biomasses were then summed for each 30 X 30 m subplot. Estimated biomass values were converted to carbon terms on a per hectare basis assuming 50 % of biomass was carbon (t C ha^{-1}).
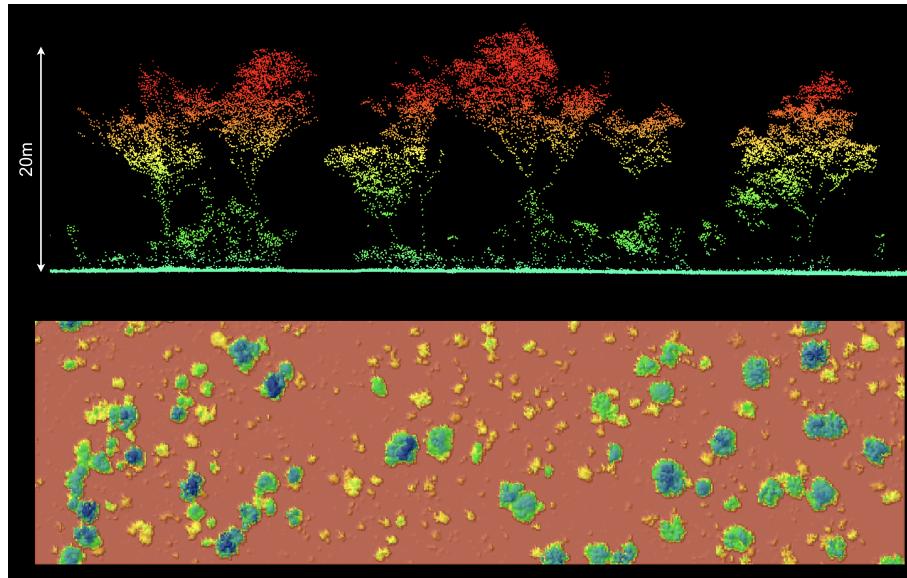
Figure 2. Cross-section through high resolution LiDAR point cloud (top) and aerial view of rasterised canopy height model interpolation (bottom).

2.2 Airborne LiDAR surveying and processing

We mapped 150 ha of the study area with airborne LiDAR in June 2013, 9 years after the beginning of the experiment. The airborne survey was conducted by Airborne Research Australia (ARA) with a full-waveform LiDAR sensor (RIEGL LMS-Q560) operated from a light fixed-wing aircraft (Diamond Aircraft ECO-Dimona). Flight-lines with >50% overlap were used

5   to achieve double coverage of the plots (average flying height 300 m AGL, swath width 250 m, line spacing 125 m), and the RIEGL LMS-Q560 was operated at 240 kHz and 135 lines per second. Slow flying speed of less than 40 ms^{-1} ensured high point densities along track, with an average return density of 22.28 m^2 and an average pulse spacing of 0.21 m.

    Raw LiDAR data were processed with RiANALYZE (RIEGL) for decomposing the full waveforms into discrete returns. The ARA RASP open source software (RASP Version 0.98: manual, code and executables available from ARA on request) was

10   used to orientate the point cloud to Cartesian coordinates and output the geolocated point cloud in the American Society for Photogrammetry and Remote Sensing (ASPRS) standard LAS format. All further point-cloud processing tasks were conducted with the LAStools suite of processing scripts (rapidlasso GmbH). The last returns were classified into ground and non-ground points for bare-earth extraction. A digital terrain model (DTM) was constructed from ground returns using a triangulated irregular network approach (TIN) at 0.25 m resolution. The DTM was used to normalize the z coordinate of vegetation returns

15   to height above ground level (Figure 2).

2.3 Upscaling aboveground woody biomass estimates with airborne LiDAR

The normalized airborne LiDAR returns were clipped to the spatial extent of each field-measured 30 X 30 m subplot. Using the *lascanopy* tool within LAStools, we extracted a suite of 14 ecologically meaningful metrics describing vegetation structure from the point cloud: mean canopy height (MCH), quadratic mean canopy height (QMCH), canopy cover >1 m (COV1), canopy cover >10 m (COV10), canopy density (DENS), kurtosis (KUR), skewness (SKE), standard deviation (SDE), canopy relief ratio (CRR), and a series of height quantiles (Q10, Q25, Q50, Q75, Q90). Using these 14 metrics as explanatory variables, we ran step-wise multiple linear regression with AIC minimization against the field-estimated biomass to identify the variables with the most explanatory power, and used them to construct a LiDAR-based biomass model. We applied the most robust model (in terms of explanatory power and RMSE) across the full extent of the airborne LiDAR coverage to examine the effects of fire treatment on aboveground woody biomass.

2.4 Statistical analyses

We digitally distributed six 30 m X 30 m quadrats in each plot for statistical comparison of treatments effects. We used a linear mixed effect modelling approach, with Gaussian residual variance, to test the significance of fire treatment on woody canopy cover, canopy height and aboveground biomass. The models were implemented in R (R Core Team 2016) with the lme4 package (Bates et al., 2014). Maximum likelihood (ML) was used to fit the models, with quadrats included as a random effect nested within fire treatments to account for possible pseudo-replication. Fixed effects were fire treatment (E1, E2, E3, E4, E5, L2, U), block position (A, B, C) and the interaction between fire treatment and block position. Models were generated for all possible combinations of fixed effects, together with a null model consisting of only the random effects of the quadrat locations. Akaikie Information Criterion (AIC) scores for each of the models were compared to identify the most parsimonious model.

3 Results

3.1 Estimation of above ground woody biomass from airborne LiDAR

Airborne LiDAR proved valuable for upscaling woody biomass measurements from the field-plots to the full extent of the fire experiment (Figure 3). Only three woody canopy structural variables were retained in the step-wise linear regression procedure: mean canopy height (MCH), total canopy cover (Cov1m), and overstory canopy cover (Cov10m):

$$AGB = -6.524 + (-0.794 Cov10m) + (-0.345 Cov1m) + (14.881 MCH) \tag{2}$$

The distribution of model residuals showed no spatial trend nor relationship with the fire treatment. The degree of residual error (RMSE = 7.35 t C ha^{-1}), provided acceptable confidence for inclusion of modelled biomass values in further analyses.
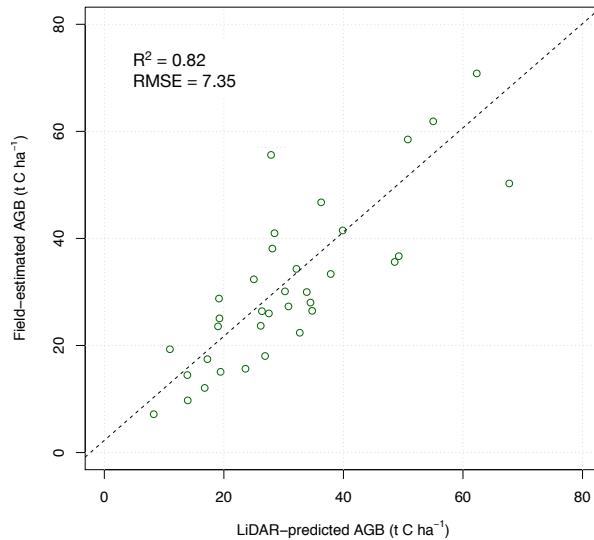
Figure 3. Estimation of aboveground biomass from airborne LiDAR.

3.2 Effects of fire regime on woody canopy cover and aboveground biomass

Canopy cover decreased along the experimental gradient of fire frequency and season, ranging from about 75 % in unburnt plots to 45 % in late season bienniel plots (Figure 4a). These differences in canopy cover translated into similar patterns of biomass variation across the experiment (Figure 4b). The highest within-treatment variability for both cover and biomass was found in the early season annual plots (E1).

The model explaining the most variation in both woody cover and biomass was one in which fire treatment, block position, and the interaction between them was included (Table 2). Model performance was poorer when the interaction term was

Table 2. Linear mixed model results of LiDAR estimated canopy cover and aboveground woody (>2m high) biomass

Model terms	AIC (Cover)	delta AIC(Cover)	AIC Biomass	delta AIC(Biomass)
Fire treatment * Block	806.14	*	864.51	*
Fire treatment + Block	855.05	48.91	903.81	39.29
Fire treatment	876.59	70.45	937.87	73.34
Block	896.81	90.67	916.23	51.70
Null model	915.34	109.20	944.09	79.57

excluded (AIC = 48.91 and AIC = 39.29). When explanatory variables were considered independently, fire treatment was more influential than block position on variation in woody cover (AIC = 70.25 vs 90.67), but not for woody biomass (AIC = 51.70 vs 73.34). These results point to an important source of environmental variation arising from block position, which represents a gradient in soil depth and moisture availability across the experimental site.

5   When we consider the spectrum of increasing fire intensity occurring across the experimental treatments, we found very strong correlations with reductions in mean woody canopy cover (R^2 = 0.968, $p < 0.001$) and aboveground biomass (R^2 = 0.758, $p = 0.014$)(Figure 5). In carbon terms, the early biennial fires caused a reduction of 10 t C ha^{-1} compared to unburnt plots, whereas late biennial fires almost doubled that reduction to 19 t C ha^{-1} (Figure 5).

3.3   Fire effects on vertical habitat structure

10   In addition to the observed patterns in woody canopy cover and aboveground biomass, our LiDAR-based assessment also revealed substantial variation in canopy height profile distributions, derived from the number of LiDAR returns from different height levels (Figure 6). Most profiles were bimodal, with a peak at 1-2 m height and a smaller peak at 10-15 m. The clearest bimodal response was found in the early season triannual burns (Figure 6c), whereas early season annual and 5-yr burn profiles were more uniform (Figure 6a,d).

15   Keeping fire frequency constant (biennial) and exploring the effects of fire season highlighted the large influence of late season versus early season burns (Figure 7). Compared with no fire, early season biennial fires reduced cover across all heights, but especially below 7m, and late season biennial fire reduced cover even further throughout, generating a vertical profile similar in shape but with much lower frequency of occurrence (Figure 7). The late season fire profile containing significantly less canopy in all height classes compared to the unburnt, but the most marked effects were in the lower height classes (shrub

20   layer).

4   Discussion

Airborne LiDAR provided direct measures of canopy cover and height distribution, and the derived metrics successfully predicted field-based estimates of aboveground biomass. The synoptic view that airborne LiDAR provided enabled us to map changes in biomass under different fire regimes, in addition to exploring differences in vegetation vertical profiles across the full expanse of the fire experiment.

4.1   Carbon storage consequences of altered fire regimes

Ten years of experimental burning imparted large structural differences in woody canopy across the plots of the Territory Wildlife Park fire experiment. Fire effects were most pronounced at the extremes of the experimental spectrum – with highest cover and biomass occurring under complete fire exclusion and lowest values obtained under biennial late season burning.

30   These trends were persistent across the underlying gradient of increasing soil depth and moisture. Recent research into woody biomass trends in the region (from long-term monitoring plots) indicate that woody biomass has been relatively stable over
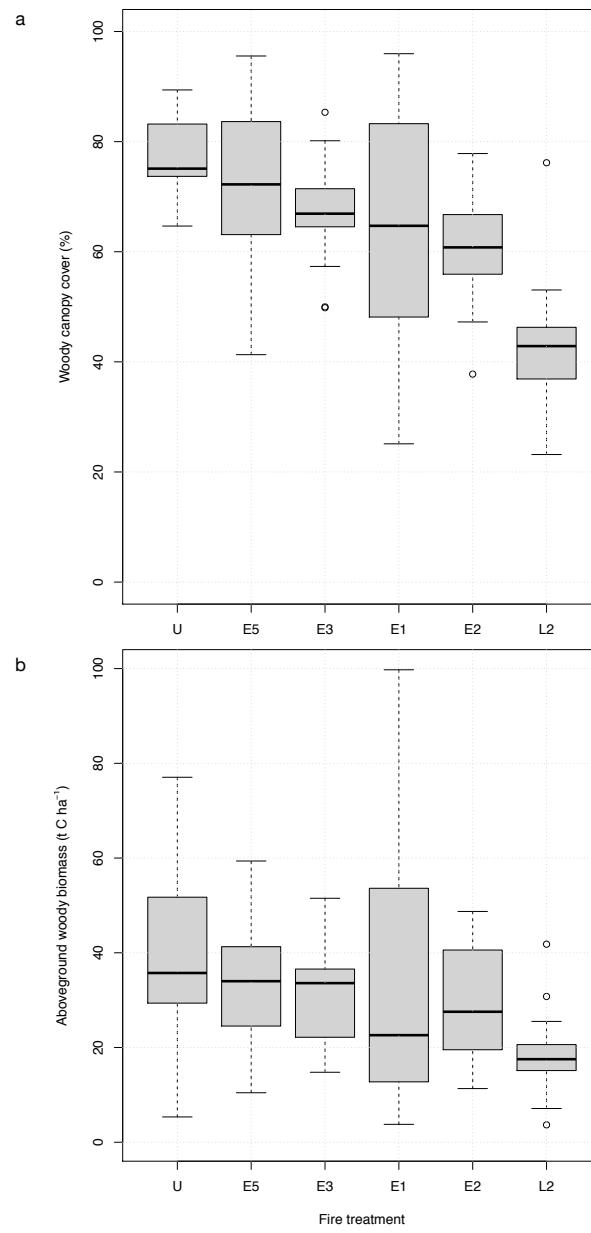
Figure 4. Relationship between fire treatments and woody canopy cover. Fire treatments ordered according to increasing fire intensity.

decadal periods, with minor evidence of woody thickening, and that biomass is negatively correlated with fire frequency (Murphy et al., 2013). However, a key finding from this study was that the observed decreases in tree biomass following severe fires were not driven by mortality of individual trees, but rather through by decreases in the rates of biomass accumulation of
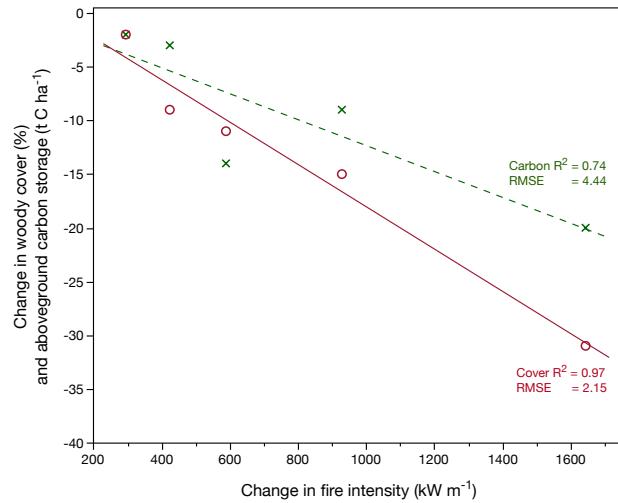
Figure 5. Correlation between in fire intensity and difference in woody canopy cover (red) and aboveground carbon storage (green), relative to unburnt plots.
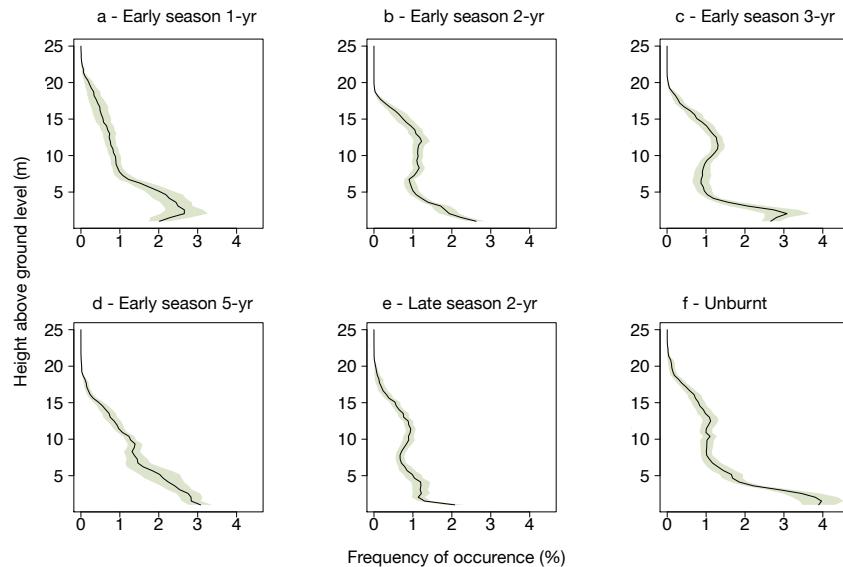
Figure 6. Effects of fire regime on 3D habitat structure determined from the frequency of airborne LiDAR returns.

surviving trees (Fensham et al., 2017). We do not have repeated individual tree data to directly corroborate this finding, but the patterns of cover and height profile reduction found in our study do suggest the consumption of trees by fire rather than just reduction in growth rates.
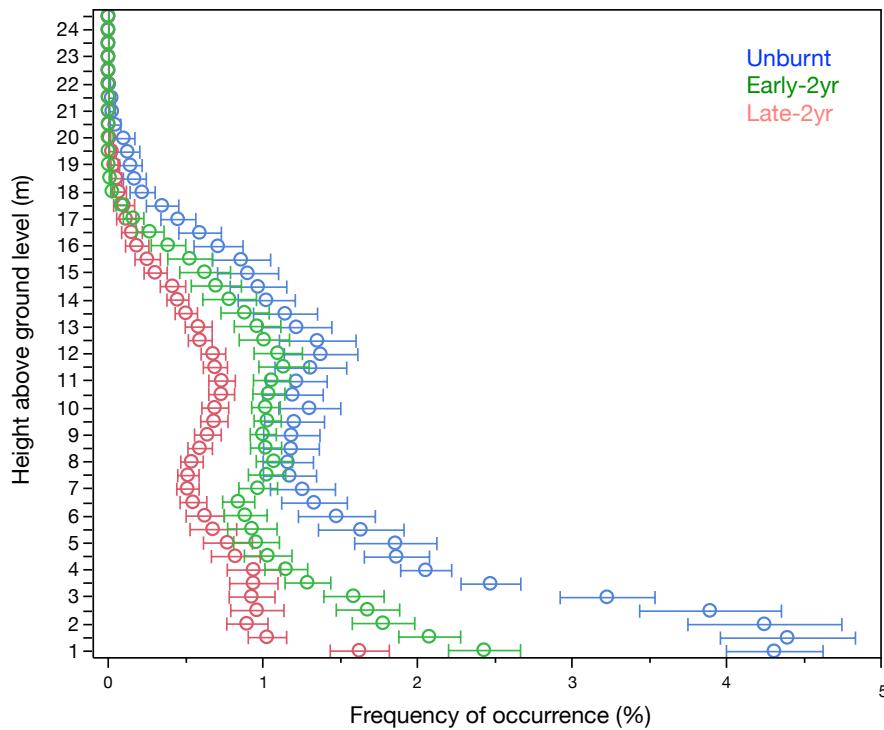
Figure 7. Effect of biennial fire season on woody vertical profile structure.

Similar investigations in southern African savannas have found that fire frequency had little bearing on woody cover, but that the presence of fire alone was a stronger predictor of reduced woody cover (Devine et al., 2015). In our study however, we found a strong correlation between decreasing woody cover and biomass with increasing fire frequency. The exception to the trend were the early biennial fires (E2), which had a slightly larger impact on structure than the early annual (E1) fires. The experimental design incorporates fire frequency and season, but the net result of these components of the fire regime is fire intensity, which is the stronger determining factor of vegetation structural change (Williams et al., 1999; Furley et al., 2008). Of all the fire treatments, the biennial burns had the highest mean intensities of 929 kW m^{-1} and 1664 kW m^{-1} for early season and late season fire respectively. These intensities are still low compared to those of large late season fires in northern Australia, and reflect the small scale of the experimental plots. Nonetheless, despite lower intensities across the board compared to larger experiments like those obtained at Kapalga experiment, our finding are in agreement with the diminished basal areas observed there under very high intensity late season fires (Andersen et al., 2003).

There is increasing interest in understanding the effect of different fire regimes on carbon stored in Australian savannas (Murphy et al., 2013; Cook et al., 2015) and recent studies (Cook et al., 2016) have shown higher carbon stocks in dead organic matter under lower fire frequencies. At the Territory Wildlife Park fire plots the early biennial fire caused a reduction of 10 t

C ha^{-1} compared to unburnt plots, whereas late biennial fires almost doubled that reduction to 19 t C ha^{-1} (Figure 5). These patterns are consistent with the trend of lower greenhouse gas emissions under early dry season fires, relative to late fires (Meyer et al., 2012) and point to the importance of available fuel load and its characteristics (greater herbaceous volume and lower moisture content late in the dry season) in understanding fire induced structural change in savannas.

5   Murphy et al. (2013) suggested that the moderation of fire regimes in northern Australia is likely to increase carbon storage in woody biomass, but the extent to which woody biomass can increase in these savannas is highly uncertain. Our results reduce some of this uncertainty, by providing quantification of the degree carbon stored in unburnt plots deviates from a range of different fire frequencies.

4.2 Shifts in vegetation vertical profile distribution under altered fire regimes

10 Different fire regimes imparted a diverse array of vertical structural profiles on woody vegetation. Although woody canopy cover and aboveground biomass displayed subtle responses among the early season fire frequency treatments, we found minimal overlap in the vertical canopy profile of the six fire regimes that we examined. Each fire regime generated a relatively unique niche space in three-dimensions, and these niches were most divergent in the understory height classes (< 5 m). Tracking these profiles over time into the future might reveal increased height of divergence as cohorts grow taller. Alternatively, 15 these understorey height curves may represent stable persistent equilibrium resprout heights that define the 'equilibrial size' of resprouts that are able to persist within the flame zone under a particular fire regime (Freeman et al., 2017).

These vertical profile findings highlight the powerful role that fire management can play in shaping three-dimensional habitat in ecosystems. The challenge this presents to land-managers is deciding which of this range of profiles is optimal for their specific management objectives. We still lack explicit understanding of how different organisms utilize three-dimensional 20 space, and it is increasingly evident that no one profile is optimal. Mid-story shrubs and trees provide key food resources for birds and small mammals, and high ground cover reduces predation risk by feral cats (Davies et al., 2016). Conversely, habitat simplification through late season burning was found to promote longer-term abundance of Frilled-neck lizards in Kakadu National Park, despite high initial direct mortality rates (Corbett et al., 2003; Andersen et al., 2005). As such, it is likely that a mix of patches at the landscape scale, spanning a diverse range of vertical profiles, is needed from a wildlife conservation 25 perspective. The relative proportions and spatial arrangement of these patches needs targeted and deeper investigation.

4.3 Limitations and future directions

Our findings in this study provide quantification of the magnitudes of fire regime effects on woody structure in a tropical savanna. When generalizing to other savanna regions however, the following limitations should be to be taken into consideration. First, prior to the establishment of the TWP fire experiment in 2004 the vegetation was unburnt since 1990. Fourteen years of 30 fire exclusion is rare in these tropical landscapes, so the starting conditions are atypical.

Second, despite the good results obtained in upscaling field-based woody biomass estimates with airborne LiDAR (Figure 3), future efforts should focus on reducing the level of uncertainty in the LiDAR-biomass model. Greater confidence in biomass/carbon prediction could be achieved by turning to individual tree-based segmentation approaches. Developments in

terrestrial LiDAR in particular show great promise for providing individual tree volumes and biomass estimates that can be scaled, together with their uncertainties, to plot and landscape scales (Calders et al., 2014; Levick et al., 2016).

Last, our analyses in this study rely on differences between treatments at a single point in time to infer the mechanisms underpinning woody structural modification. Although typical for this type of investigation, the single time-point approach should ideally be complimented with time-series analyses of before and after fire events to better constrain the mechanisms underpinning structural change.

5 Conclusions

We quantified the magnitude of aboveground carbon reduction under different regimes by integrating airborne LiDAR, field-surveys, and a long-term fire regime experiment. Our results highlight the impact of late season burning on both carbon storage and on canopy vertical profile heterogeneity. Clear relationships between biodiversity and fire regimes have proven difficult to establish in savannas, despite many attempts at linking floral and faunal diversity directly to fire regime patterns. The range of vertical profile responses that we have illustrated here under different experimental fire treatments could hold the key to unlocking stronger links between fire management and biodiversity responses. High-resolution LiDAR can expose the structural consequences of different management actions and make them more easily accessible for integration with biodiversity and ecosystem process studies.

Competing interests. The authors declare no competing interests.

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