Original reviewer comments are in black text

Author response comments are in blue text.

Reviewer 1

Reviewer comment: This manuscript reports the effects of various fire treatments, including combinations of early/late season burning and variation in fire frequency over more than a decade, on aboveground vegetation biomass and structure in a savanna habitat in northern Australia as quantified by airborne lidar. The results are relatively straight-forward and offer quantitative data that may be useful in future models of carbon dynamics and management of vegetation structure or heterogeneity.

Author response: Thank you, we do hope that this work proves useful to the modelling community.

Reviewer comment: There is an interesting spatial interaction effect in which the results of a fire treatment depend on soil moisture and soil depth; the paper would be improved if these results were further explored and elaborated upon. I would have appreciated seeing a validation of their model results on out-of-sample data to assess the accuracy of their results and the significance of the soil depth/moisture gradient.

Author response: We agree with the points you have raised and have addressed them in detail in the specific comments section below.

Reviewer comment: Some of the conclusions with respect to what is driving the observed decreases in woody cover with increasing fire intensity (i.e., greater tree mortality or reduced accumulation of woody biomass) appear to be unsubstantiated and require further explanation.

Author response: We have modified the sections in question for clarification.

Reviewer comment: Overall the paper, while not especially novel, does represent an important contribution to the literature by quantifying the effects of various fire regimes on 3-dimensional structure and aboveground biomass in northern Australian savannas.

Author response: Thank you for your comments, they have helped shape a much stronger manuscript.

Reviewer comment: In the abstract there are inconsistent statements about the temporal scale of the experiment and how to interpret the results with respect to time. On page 1, line 3 the experiment is referred to as 'long-term', whereas on page 1, line 12 the results as said to have occurred over time scales as 'short' as a decade. It is important that the authors represent a consistent message: in their expert opinion, do structural changes occurring over a decade represent short-term or long-term responses? The title suggests that the interpretation is one that these are rapid changes and therefore observing these plots over ten years is not a particularly long time in the savanna tree cover cycle.

Author response: Very true, thanks for highlighting this. We tend to think of the experiment as a long-term one as we plan to maintain it for decades to come. However we agree that the current timespan of the experiment is short in context of savanna tree cover cycles, which is why we were impressed with the degree of change that has occurred and used 'rapid' in the title. We have made changes to our terminology throughout to avoid this ambiguity and no longer refer to it as a long-term experiment.

Reviewer comment: Page 2, lines 11-22: While declines in faunal populations are certainly important, I was surprised by the one-sided discussion of negative effects of savanna fires (e.g., the effects of savanna fires on greenhouse gas emissions). I felt this section of the manuscript lacked a balanced discussion of fire as an evolutionary force in savannas that, when suppressed, can have negative effects on savanna flora and fauna. True that some faunal populations are influenced but what about savanna specialists or species that rely on grass cover? Are there no species in these savannas that benefit from fire? Given the global and historical significance of fire in savannas, I advocate for a more balanced discussion of fire as a natural part of savanna landscapes that, when well-managed, can have beneficial effects.

Author response: Good point. It was certainty not our intention to present fire as being detrimental for savannas. We added to this section to present a more balanced perspective, including the importance of fire in savanna ecosystem functioning.

Reviewer comment: Page 2, lines 28-29: Is the significance here only that the approach is novel for savannas? Because lidar has been used to study fire effects in many other systems. Also, why is Smit et al. 2010 and your 2009 paper (Levick et al. 2009) not credited with studying fire effects on savanna vegetation structure using lidar? The Smit et al. 2010 paper was squarely aimed at ". . .assessing vegetation biomass and structural diversity responses to experimental fires"

Author response: The Smit et al 2010 and Levick et al 2009 papers are credited here since they utilised airborne LiDAR across fire experiments in savanna, but neither of these papers quantified biomass and its difference across fire treatments (only height and cover).

Reviewer comment: Page 2, line 34: aim 1 is somewhat weak considering that lidar has been used successfully to study vegetation biomass and structure in so many other systems. It seems that we already know the answer to the question about reliably detecting vegetation and biomass and structure by airborne lidar is 'yes'. This first aim also puts the emphasis of the paper on methodology and thresholds of detection, which, in my opinion, changes the nature of the paper and requires more of a methodological approach. My suggestion is to leave this part out of future versions and focus on the effects of fire in this system.

Author response: Thank you - valid comment. The key issue here how subtle a change in structure can be detected (signal-to-noise ratio). However, the goal here was indeed to focus on the fire effects, so we have restructured the aims to focus more squarely on the ecology. We agree that the answer to reliable detection of vegetation structure by LiDAR is "yes" – but what needs deeper consideration is the sensitivity of these techniques to detecting change. In our case, is the degree of structural change caused by fire manipulation greater than the uncertainty associated with LiDAR biomass estimation? We have focused on this in the discussion rather than upfront as suggested.

Reviewer comment: Page 3, Table 1: This table legend is incomplete – are these mean fire intensity values? Also, I suggest you include standard errors or ranges for the fire intensity values (i.e., range for E5 and +/- SE for others).

Author response: Updated as suggested, with SE included.

Reviewer comment: Page 4, eqn (1); is there a different equation for multi-stemmed shrubs? Are they a significant part of the carbon pool?

Author response: Very good question. Shrubs are generally ignored, and are considered to be a minor part of the carbon pool. However they are an important part of the ecosystem and some represent future trees. We have not accounted for shrubs well in either our fieldwork or our airborne LiDAR. We have now made this clear in the manuscript and have added it to our limitations section. As a side note we have started new projects exploring the shrub component with ground-based LiDAR.

Reviewer comment: Page 6, lines 8-10: this seems like a very comprehensive model which fits the data well (e.g., Fig. 3), but I am worried that there was no validation on out-of-sample data, which is the gold standard of model assessment. Perhaps it is challenging due to the paucity of lidar data, but is there any capacity to validate the model on out-of-sample data to get a better sense of model accuracy? It will also provide a means to understand the generality of eqn (2) to represent aboveground woody biomass with lidar derived data from this study (versus having to derive a new eqn for woody biomass at a different site).

Author response: We agree that out-of-sample data would be ideal for further independent validation. Unfortunately this is not possible with the data we have, and with the time that has passed since the LiDAR flight was conducted. Despite this, we have added our field estimated C values to Figure 4b so that the value for each 30 m X 30 m plot is now overlaid on top of the LiDAR derived values in the box plots. A key point here is that interpretation of biomass changes across the fire treatments does not differ if using the original field data or the LiDAR derived model – providing greater confidence in the ecological conclusions we are drawing.

Reviewer comment: Page 7 and results section throughout: I strongly advise that when values are being reported, such as 75% or 45% canopy cover, the authors include some reasonable representation of error or variation (be it standard error or standard deviation, doesn't matter).

Author response: Updated as suggested.

Reviewer comment: Page 7, Fig. 3 legend: text is incomplete. One should be able to look at the figure and legend and understand what information is being conveyed. This figure legend leaves much to be desired (location, sample size, where the data came from, refence to the model, etc.).

Author response: Agreed – updated accordingly, and figure legends improved throughout.

Reviewer comment: Page 8, lines 1-4: I found the fire * block interaction to be very interesting and worthy of some further exploration or analysis. I think your audience would be interested to know more about this interaction – are there other ancillary data that could help you explore this soil/moisture effect? To begin with, the directionality of the interaction is never reported – does greater depth/moisture increase or decrease the effect of a given fire treatment on woody cover and biomass? At the very least this should be reported. Further, once the directionality is presented, what is the mechanistic nature of this interaction? Is it related to quantity or composition of the fuel as depth and soil water availability changes? This question would be helped by data if you have it, otherwise perhaps a few sentences in the discussion are in order.

Author response: Very good point – we have expanded on this interaction and have made the directionality clear. We have also updated Figure 5 to illustrate the block interaction more clearly.

Reviewer comment: Page 8, lines 22-24: like my comment above, I did not find this conclusion or aim very compelling since we already know these methods work well and this is not a methods paper. I recommend sticking to the ecological effects of fire in these tropical savannas as the main focus of the paper.

Author response: Agreed – we have restructured the aims to focus squarely on the ecological effects.

Reviewer comment: Page 8, line 30: is this interpretation entirely correct? Wasn't there an interaction effect between fire treatment and block suggesting that the fire treatments did not simply 'persist' but in fact 'changed' with soils moisture and depth (i.e., the interaction effect). I suggest a re-evaluation of this simple interpretation and better presentation of what are interesting interaction effects.

Author response: Thanks for picking up this point – agreed and modified as suggested.

Reviewer comment: Page 9, lines 2-3 and page 10, lines 1-3: I do not understand how this conclusion (that decreasing biomass was the result of decreasing biomass accumulation rather than mortality) was reached from this study. The text and the citation of Fensham et al. 2017 suggests that the result and conclusion come from another study rather than this one – is that the case? Moreover, the statement on page 10 is confusing because it suggests that your interpretation of the data is that mortality from fire is a driving factor in the observed patterns (in direct contracts to the sentence on page 9). Either way, clarification and rewriting are required here, as we don't know where these conclusions are coming from and there is no evidence that the current study can provide demographic data of the nature being described here.

Author response: It was not our intention to suggest that decreasing biomass accumulation rather than mortality was the driver. In hindsight we can see how it could have been read like this and have modified this section to avoid any confusion. Likewise we have rewritten these sentences to remove ambiguity between interpretations from our study and the literature referenced.

Reviewer comment: Page 10 & 11: If my interpretation is correct, Figs 6 and 7 are representing the same data. Consequently, it may make more sense to represent Fig. 7 as a difference from the control plot rather than as the same data presented in Fig. 6 (would that make sense?).

Author response: They are similar although Figure 6 showed mean vertical profile and 95% CI for all treatments, while Figure 7 shows only unburnt, 2 year early season and 2 year late season with SE of the mean. We have tried the suggestion of plotting Figure 7 as the difference to the unburnt, however we consider the direct comparison of the unburnt condition and the different season burns to be valuable. We have expanded and clarified the figure legends.

Reviewer comment: Page 7, Table 2: delta AIC for the top model should be reported as 0.00.

Author response: Thank you – corrected.

Reviewer comment: Page 8, line 27: should read "...in woody canopy cover..." or "...in woody canopy structure. . ."

Author response: Fixed.

Reviewer comment: Page 10, Fig. 5 legend: should the legend read: "Correlation between change in fire intensity and difference in woody canopy cover. . ."? Also, it needs to be clear what is meant by change in fire intensity; is this control – treatment or some other metric. More text and greater clarity (which is the case with almost all the figure legends in this paper).

Author response: Thank you, modified this figure and have clarified the legend, providing more detail.

Reviewer 2

Reviewer comment: This is a useful application of LiDAR technology to examine effects of burning on vegetation structure. The results are important, but I must admit that I was disappointed there were no analyses of how fire affected 3D vegetation structure, despite multiple claims to the contrary (Page 1, lines 8 and 11; Page 2, line 34; Page 12, Line 13; Page12, line 17 Figure 6, caption). These claims should be removed or actual analysis of 3D structure should be added.

Author response: Thank you, we're glad you consider these results to be important. Our reference to 3D comes from our consideration of canopy cover (horizontal component) and height (vertical component) which together encompass the 3D structure of vegetation. However we agree with your comment that we have not analysed single metrics that capture 3D structure/diversity. We have removed any misleading claims and have checked the validity of our terminology throughout.

Reviewer comment: Figure 2 is a great reconstruction of the 3D structure of the vegetation, but the information contained therein was ultimately distilled into metrics that lose this 3D information. I do not have the expertise to suggest what metrics should be used to compare 3D structure, but certainly such metrics must exist, such as the various methods to measure aggregation.

Author response: Thanks you. We disagree that the 3D information has been lost through our analyses, it has been distilled and we focused on metrics which are targeted in traditional ecology (height, height layering, cover, biomass). The field of true 3D metrics is gaining momentum and we agree more could be done to derive metrics of full 3D structure. We consider this avenue to be important for future research, but beyond the scope of this study. We have raised this point in the future directions section of our discussion.

Reviewer comment: It would have been helpful to have a brief overview of the research approach at the end of the introduction. For example, as I was reading the methods, it was not clear to me why you used Lidar to estimate biomass of the fire plots when you already had more direct measurements of above- ground biomass for the same plots. Of course your approach allowed you to estimate biomass for a 3-fold greater area of each experimental plot, which I suspect is the reason that you did this, but this was not clearly laid out.

Author response: Thanks for pointing that out, and yes our reasoning to use LiDAR was to increase the area sampled, but also to test the potential for LiDAR to be used in future fire/biomass studies over much larger areas in these landscapes. We have laid this out more clearly at the end of the introduction.

Reviewer comment: Considering that you possess the ground-based data for comparing fire impact on AGB, a direct test using these data should be included. Even though the area sampled is lower, the ground measurements avoid the additional error introduced by relying on a model relationship (even though the fit was quite good).

Author response: Good point - we have added the field estimated AGB values to Figure 4b, making it possible to compare the patterns as if we only had field data available.

Reviewer comment: What is the difference between Figure 7 and the corresponding data from figure 6? At first glance, it appeared that Figure 7 was presenting data already presented in figure 6, but upon close examination, the corresponding data in figure 6 are different than figure 7. For example in figure 6, there is more vegetation at heights of about 8 to 15m in the 2-yr early treatment than in the unburnt treatment, in contrast to Figure 7. The figure legends and text do not help clarify these differences. Also, are the error bars standard errors? Were they calculated using variation and n of 30x30 plots or of experimental plots? The latter should be used if we are to use them to compare treatments.

Author response: It is the same underlying data. We have tried various iterations of showing all the profiles together, but found them too clustered for comparison. Figure 6 shows the vertical profile means and 95% CI. We broke out the unburnt and the early and late season 2-years to show the effect of altering only season while keeping only frequency constant, since early versus late season burning is important from a policy perspective in northern Australia. We also show the mean and SE (experimental plots) here to be more objective is comparing the overlap between treatments. Clarified in text and legends.

Reviewer comment: The fire intensity data in Table 1 are important for this study, but no details are given. How were these data collected? Were they obtained for every fire between 2004 and 2013 or just for representative fires? If these data have not been published elsewhere then the methods should be described.

Author response: We have added this information to the methods section and provided a reference to earlier work establishing the technique.

Reviewer comment: Page 2, Line 23. It seems like an overstatement that detailed 3D measurements are the best way to quantify carbon dynamics. Perhaps it could be the best choice for non-destructive measurements of certain C pools.

Author response: True – modified to say that it is an avenue for gaining deeper understanding of above ground biomass.

Reviewer comment: Page 3, line 15 and line 19. In these instances replace "blocks" with "block."

Author response: Corrected.

Reviewer comment: Page 4, line 3. In what year were these tree measurements made?

Author response: 2014 – now specified in manuscript

Reviewer comment: Page 5, lines 8-12 and page 6, line 3. Are references available for these software tools?

Author response: Yes – now provided. rapidlasso GmbH, "LAStools - efficient LiDAR processing software", obtained from http://rapidlasso.com/LAStools

Reviewer comment: Page 6, line 12. I presume that two of these six quadrats corresponded with the plots sampled on the ground. It would be helpful to clarify this. If not, I am not sure how figure 3 was generated.

Author response: Correct – clarified.

Reviewer comment: Page 6, line 15. I disagree that including quadrats as a random resolves the issue of pseudoreplication. One foolproof way of avoiding pseudoreplication would be to average your data across quadrats to get a single value for each experimental plot. Traditionally the blocks are considered to provide the replication, but this is lost if block and block x treatment are treated as a fixed factors. For a randomized full block design, block is typically treated as a random factor, treating the blocks as replicates of the experimental treatment, and in a least-squares approach, the block x treatment interaction would be used for the denominator MS. Of course the denominator df would be rather small in a design like this. I am not quite sure what is accomplished by treating the subplot as a random factor, but certainly it is not eliminating the pseudoreplication issue. I believe there are ways of estimating df for lme4 tests, and these should be presented, and I strongly recommend that the authors archive their data and r code as supplementary information. All this being said, this is a large-scale experiment, which commonly suffer from pseudoreplication, so I am not as concerned about pseudoreplication here as I am about the claim that pseudoreplication has been avoided.

Author response: Thanks for raising these concerns. We have removed claims that our approach has avoided pseudoreplication.

Reviewer comment: Figure 3. The legend should state what each point represents. I presume the ground-estimated AGB corresponds to one 30m x 30m plot.

Author response: Yes that's correct. We have updated this legend (and others) with more detail.

Reviewer comment: Page 7, line 6-7. I don't think is what you really mean to say. It is always true that the model including all factors and interactions will explain the most variance. Besides, Table 2 doesn't really show how much variance is explained.

Author response: Thanks for picking this up – we have reworded the text.

Reviewer comment: Page 8, line 18. It is stated here that the late burns had significantly less canopy than the unburnt, but no statistical tests were performed. Perhaps this conclusion is based on the non-overlap of error bars in figure 7. This should be clarified, and it is important to provide details on how these errors bars were generated.

Author response: Clarified as suggested, and details on error bars suggested.

Reviewer comment: Page 9, Line 2. It isn't clear what "this study" is. Does it refer to the present study, to Murphy et al 2013, or to Fensham et al 2017?

Author response: Thanks – we have clarified this section.

Reviewer comment: Figure 5. Are these relationships significant if you do not aggregate them by treatment? Presumably you have fire intensity data for each 1-ha plot, which would allow you to test this for a larger number of true replicates.

Author response: Good point – we have explored this in more detail and have used the non-aggregated intensity data. The refreshed Figure 5 now also shows the differences with landscape position as raised by Reviewer 1 (A,B,C block).

Reviewer comment: Reviewer comment: Page 10, Lines 1-3. Please be specific about what results from your study suggest this.

Author response: Clarified as requested.

Reviewer comment: Figure 6. Please provide more information about the data in this figure. Are these frequency distributions of the returns themselves, or are they a reconstruction of vegetation density that takes into account the fact that foliage high in the canopy has a higher probability of being detected than foliage low in the canopy. Also, figure 6 shows 1-D vegetation structure, not 3-D structure as indicated by the caption.

Author response: We have provided clearer information as requested. These are the returns after running a voxel thinning to remove duplicate points and standardise density across the site. Probability of upper layer detection is not explicitly accounted for - these effects are minimal in savannas compared to denser tropical or temperate systems. These details have been added and the Figure legend has been corrected.

Reviewer comment: Page 11, Line 3. Where do you show this correlation? You show a relationship with fire intensity, but I don't think you showed this for frequency.

Author response: True – we were referring the trends in Figures 4, and have revised the sentence.

Reviewer comment: Page 12, line 3. This mention of herbaceous volume here raises a relevant point regarding the interpretation of your figures. In figure 7, do the data corresponding to 1-m above the ground correspond in reality to 0-1 m, or to 1-2 m, or to 0.5 to 1.5 m. When looking at figure 7, it wasn't clear whether grasses would be included in the lowest point.

Author response: 1-m corresponds to 1-2m, we have clarified this in the Figure legend. Denser patches of grass may be included in the lower layers, but most often it is not detected. We have added a line stating there might be some returns coming from herbaceous layer, but we cannot quantify this.

Reviewer comment: Page 12, line 12. I am not sure what minimal overlap means here. I don't think you are referring to overlap of individual trees, since you did not examine this. And looking at figure six, I would say that there is a lot of overlap in these distributions, since some distributions fit wholly within others.

Author response: Thanks for picking this up – we did mean the distributions, but overlap was the wrong term, we have clarified this sentence.

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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 vertical habitat structure and 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~~ canopy 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 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. The magnitude of fire effects on vegetation structure varied along the environmental gradient underpinning the experiment, with less reduction in biomass in plots with deeper soils. Our results highlight the large extent to which fire management can shape ~~3D~~ woody 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 conservationand carbon sequestration~~/habitat conservation, carbon sequestration, and emission reduction initiatives in the region.

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, enabling 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).

~~High three-dimensional~~ 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). ~~Fire-driven structural changes in~~ 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. ~~The structural modifications that fires impart on~~ 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). ~~Quantification of fire induced~~ Despite the importance of quantifying fire induced changes to 3D ~~structural changes~~ structure in savanna vegetation~~is lacking however, and~~ , 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 (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~~(Lawes et al., 2015; Legge et al., 2015; Woinarski et al., 2015)~~, 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 Australias national greenhouse-gas accounts, and are responsible for approximately 3% of total accountable greenhouse-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 certain components of 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, 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. While much attention is currently being given to reducing the extent and frequency of late season fires in northern Australia, it is important to recognise that savannas have evolved with fire (Bond and Keeley, 2005; Durigan and Ratter, 2016) and excluding fire would be detrimental to certain savanna specialists that favour more open and grassy habitat. The challenge is finding the best mix of patches of different regimes across connected landscapes.

~~An understanding~~ Understanding of how different fire regimes impact habitat structure and carbon dynamics in tropical savannas ~~is best achieved~~ can be enhanced through detailed 3D measurements of vegetation structure at sites subject to long-term, replicated experimental fire treatments. Traditional field-based inventory techniques are limited in their ability to quantify

3D structure, but light-detection and ranging (LiDAR) can now ~~do~~ 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.

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 of vegetation structure 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 borne LiDAR; ii) how vegetation structural diversity and carbon storage~~ explore how vegetation carbon storage and structural diversity respond to increasing fire frequency; and ~~iii)~~ ii) quantify the structural impact of ~~higher-intensity,~~ late-season fires compared to early-season fires. We use airborne LiDAR data to provide greater spatial coverage than can be achieved with field sampling alone, and to gain better understanding of how reliably LiDAR could be used to assess savanna carbon dynamics in instances where field data may not be available or attainable.

2 Methods

2.1 Study site and experimental design

The Territory Wildlife Park is located 40 km south of Darwin in ~~Australia~~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, 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 ~~ř~~°C and 20.9 ~~ř~~°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 1). Soil depth increases from north to south, and the C ~~blocks have~~ block has higher soil moisture given ~~their~~ its proximity to a small ~~creek~~ drainage line. Six fire treatments were randomly assigned to each block at the start of the experiment: unburnt plots (U) 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~~ block only).

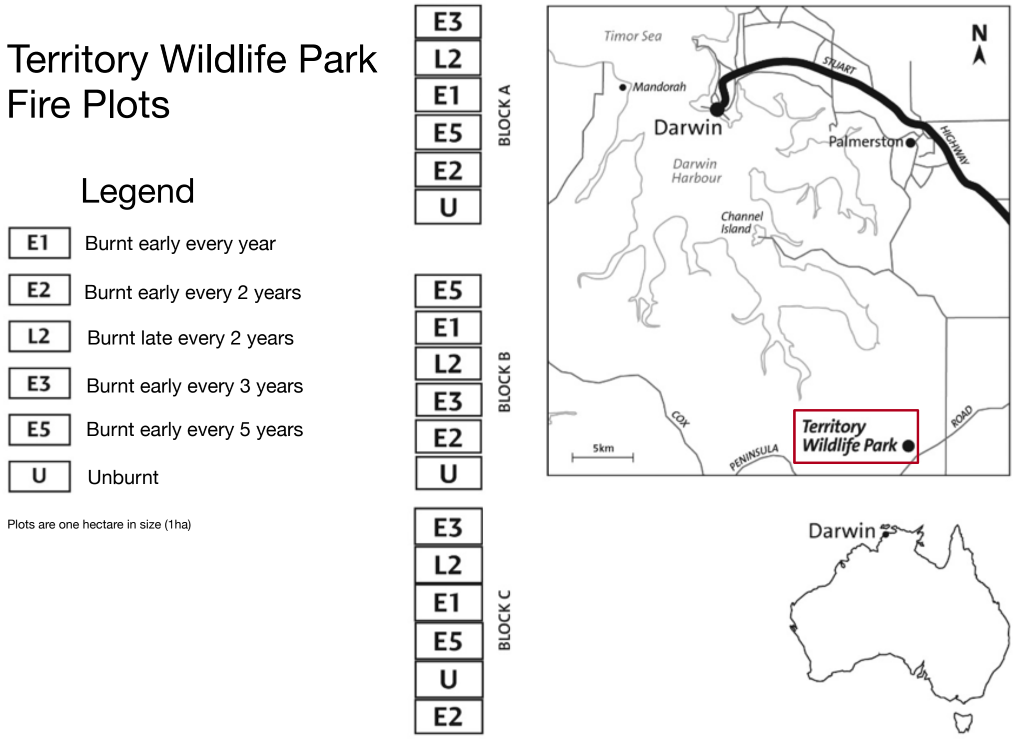

Figure 1. Location and experimental design layout of the Territory Wildlife Park fire manipulation experiment. Treatments were fist implemented in 2004. Soil depth and soil moisture increases from the northern to southern blocks.

During each experimental burn, fire intensity was estimated using the established relationship between rate of spread and fuel load (Williams et al., 1998). Rate of fire spread was determined from thermocouples linked to electronic stop watches positioned 5 cm above the soil surface, in the flaming combustion zone. Six timers were used in each 1 ha plot, arranged in a series of equilateral triangles, with 10 m sides. The rate of fire spread was also determined by observers using stop watches, manually recording the time of arrival at the points where the electronic watches were positioned. All points were marked by star pickets and flagging tape. Fuel loads were determined prior to each fire by direct harvest and weighing. Ten replicate 0.5 m x 0.5 m fuel samples were cut for each plot. Fuel heat content was assumed to be 20 000 kJ per kg dry weight.

2.1.1 Field-based estimation of above ground woody biomass

2.2 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

Table 1. Fire regime characteristics of the Territory Wildlife Park experimental site. Data are for the period 2004-2013. Fire intensity values are the mean and standard error over the course of the experiment.

Treatment	Season	Frequency (yrs)	Intensity (kW m^{-1})	Times burnt
E1	June	1	589 $\pm$144	9
E2	June	2	929 $\pm$20	4
E3	June	3	424 $\pm$26	3
E5	June	5	295 $\pm$69	2
L2	October	2	1644 $\pm$131	5
U	n/a	0	0	0

recorded. The location of each individual plant was recorded to 0.3 m accuracy using a differential GPS with post-processing (Trimble Inc.). The health of each plant was recorded on a scale from 1 (healthy) to 5 (dead). Heights 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):

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

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}). This approach did not consider the contribution of small (<2 m) multi-stemmed shrubs to the carbon pool.

2.3 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 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 m-1 s 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 Laser Measurement Systems GmbH) for decomposing the full waveforms into discrete returns. The ARA RASP open source software (RASP Version 0.98: manual, code and executables

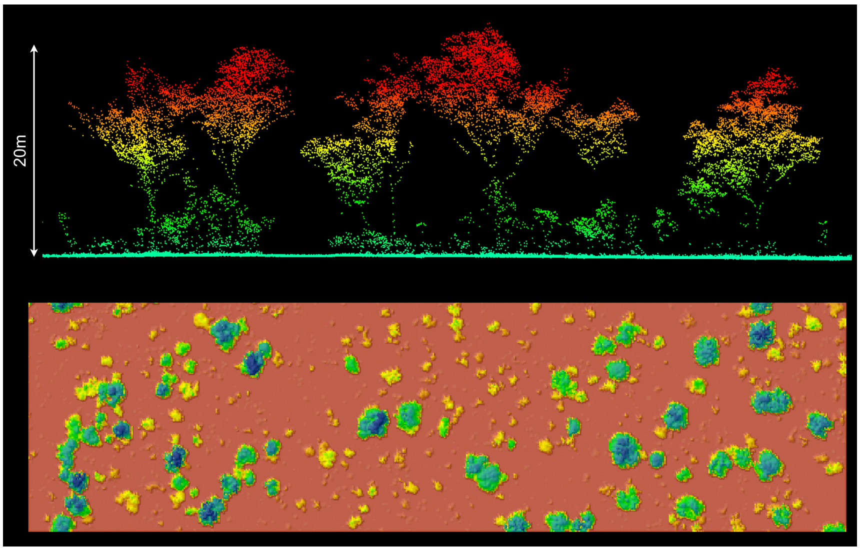

Figure 2. Cross-section through high resolution LiDAR point cloud (top) and aerial view of ~~interpolated~~ rasterised canopy height model (CHM) interpolation (bottom). The LiDAR point cloud provided excellent representation of both the vertical and horizontal structure of vegetation across the site.

available from ARA on request) was 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~~ *z* coordinate of vegetation returns to height above ground level (Figure 2).

2.4 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~~ *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.

2.5 ~~Statistical analyses~~Assessment of treatment effects

We digitally distributed six 30 m X 30 m ~~quadrats~~ subplots 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~~ subplots 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):

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

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.

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 % (SE = 1.7) in unburnt plots to 45 % ~~at L2~~ (SE = 2.3) 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~~and E5 plots~~).

The ~~model explaining the most~~ best model explaining 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 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 ~~the reverse was true~~ 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.

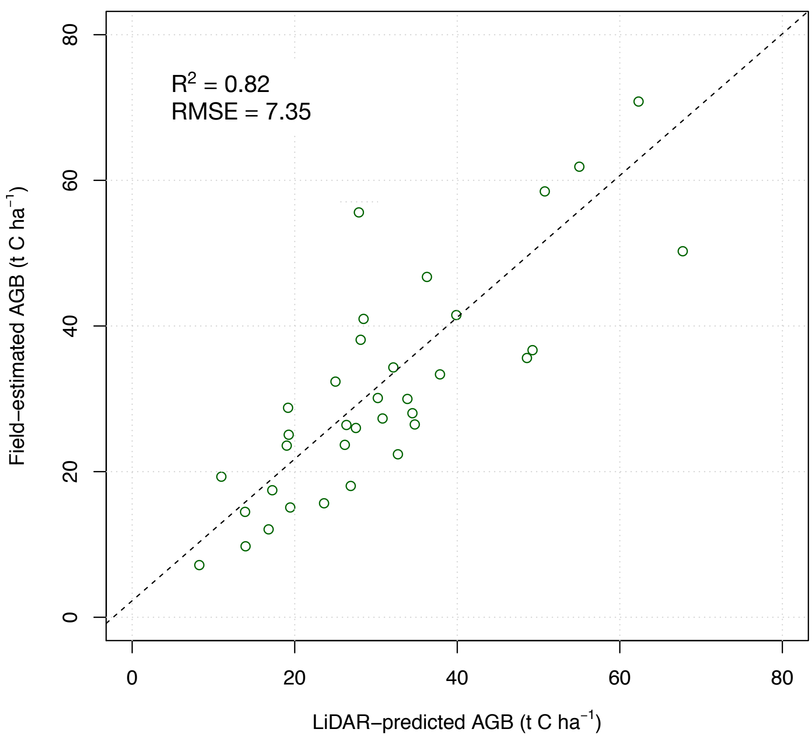

Figure 3. ~~Estimation of~~ Relationship between field-estimated aboveground biomass and estimates predicted from airborne LiDAR metrics. Open green circles represent individual subplots (30 m X 30 m), dashed line shows the liner fit.

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

Model terms	AIC (Cover)	delta AIC(Cover)	AIC Biomass	delta AIC(Biomass)
Fire treatment * Block	806.14	~~*~~ 0.00	864.51	~~*~~ 0.00
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

When we consider the spectrum of increasing fire intensity occurring across the experimental treatments, we found that correlations between the reductions in aboveground biomass and fire intensity decreased along the soil depth and moisture availability gradient (Figure 5). In carbon terms, the early biennial fires on average 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}.

3.3 Fire effects on vertical habitat structure

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).

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 ~~at~~ across all heights, but especially below 7m, and late season biennial fire reduced cover even further throughout, ~~but especially in the mid and upper canopy~~ generating a vertical profile similar in shape but with much lower frequency of occurrence (Figure 7). The late season fire profile contained significantly less canopy in all height classes compared to the unburnt (no overlap of error bars), but the most marked effects were in the lower height classes (shrub layer).

4 Discussion

Airborne LiDAR ~~metrics~~ 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 ~~model~~ 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

~~We observed major~~ Ten years of experimental burning imparted large structural differences in woody canopy ~~structure across the~~ across the plots of the Territory Wildlife Park fire ~~plots after ten years of experimental burning~~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 of woody canopy structure obtained under biennial late season ~~burn. Recent research from~~ burning. The directionality of these trends was persistent across the underlying gradient of increasing soil depth and moisture, but the magnitude and slope of the effects was greater in the A and B block with shallower, drier soils (Figure 5). The lower magnitude of carbon reduction in the lower lying "C" block likely stems from the sparse herbaceous cover in these plots which results in patchy, low intensity fires.

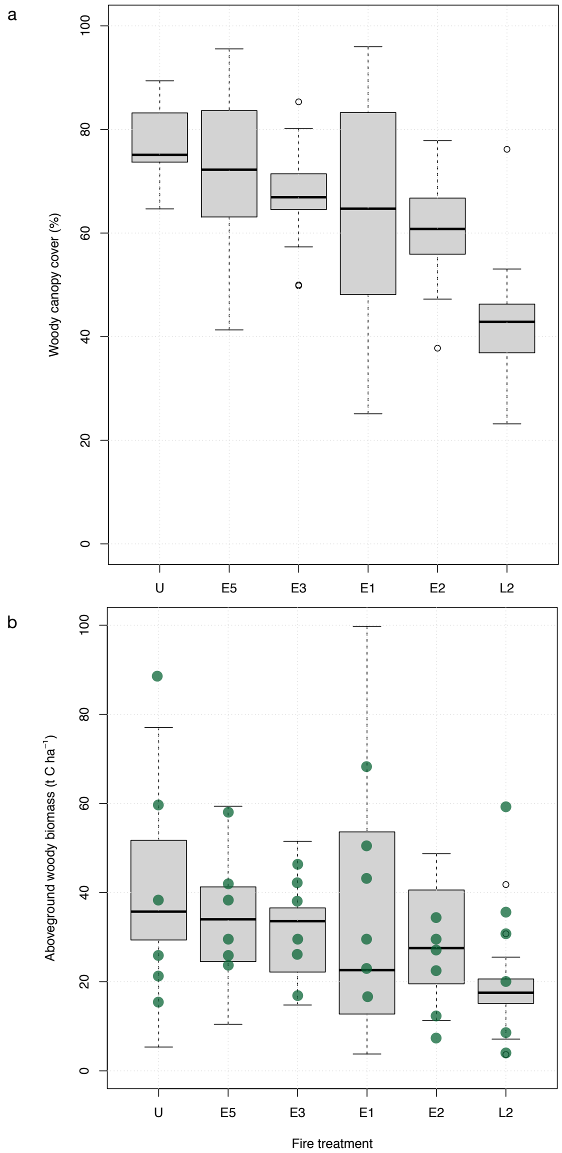

Figure 4. Relationship between fire treatments and (a) woody canopy cover and (b) woody biomass. Fire treatments ordered according to increasing fire intensity. Green dots in (b) indicate field values derived from 30 m X 30 m subplots.

Recent research into woody biomass trends in the region (from long-term field monitoring plots) indicate that woody biomass has been relatively stable over decadal periods, with minor evidence of woody thickening, and that biomass is negatively

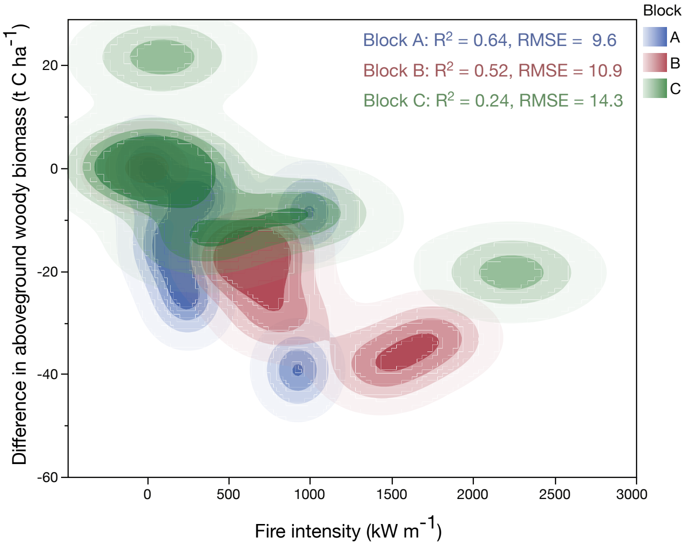

Figure 5. Density plot showing the relationship between increasing fire intensity reduction in woody carbon storage, relative to unburnt plots, for the A (blue), B (red) and C (green) Blocks.

correlated with fire frequency (Murphy et al., 2013). However, as Fensham et al. (2017) note, a key finding emerging from that regional study was that the observed decreases in tree biomass following severe fires were not driven by mortality of individual trees, but rather by decreases in the rates of biomass accumulation of surviving trees. We do not have repeated individual tree data in our study to directly corroborate this finding, but the patterns of reduced cover throughout the height profile do suggest mortality and the consumption of trees by fire, rather than just reduction in growth rates.

Similar investigations in southern African savannas have found that fire frequency itself 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 ~~, we did find a general trend of decreasing woody~~ however, we found that cover and biomass ~~with increasing fire frequency . The~~ were reduced as fire frequency increased (Figure 4), with the exception to the trend ~~were~~ being 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). ~~When we consider the spectrum of increasing fire intensity occurring across the experimental treatments, we observe 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).~~ Of all the fire treatments, the biennial burns had the highest mean intensities of 929 kW ~~m-1~~ m^{-1} and 1664 kW ~~m-1~~ 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

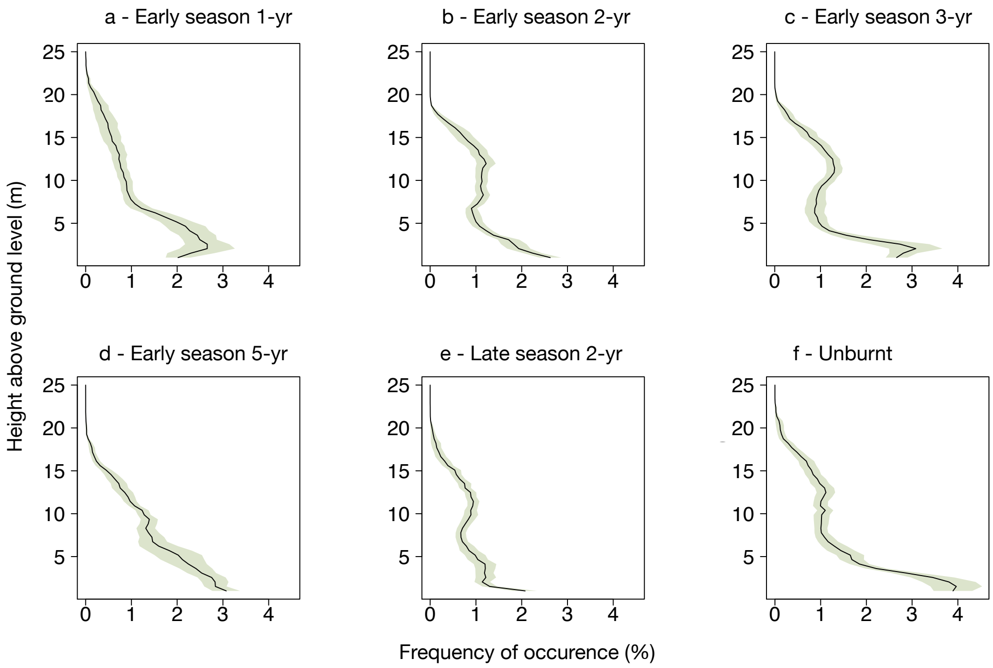

Figure 6. Effects of fire regime on ~~3D~~ vertical habitat structure determined from the frequency of airborne LiDAR returns. Solid black lines are the mean frequency distribution of LiDAR returns, and the green bands indicate the 95% confidence interval.

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~~ ha^{-1} on average compared to unburnt plots, whereas late biennial fires almost doubled that average reduction to 19 t C ~~ha-1~~ 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. This is further emphasised by the variation in response to fire along the environmental gradient of the experimental site.

~~Correlation between in fire intensity and difference in woody canopy cover (red) and aboveground carbon storage (green), relative to unburnt plots.~~

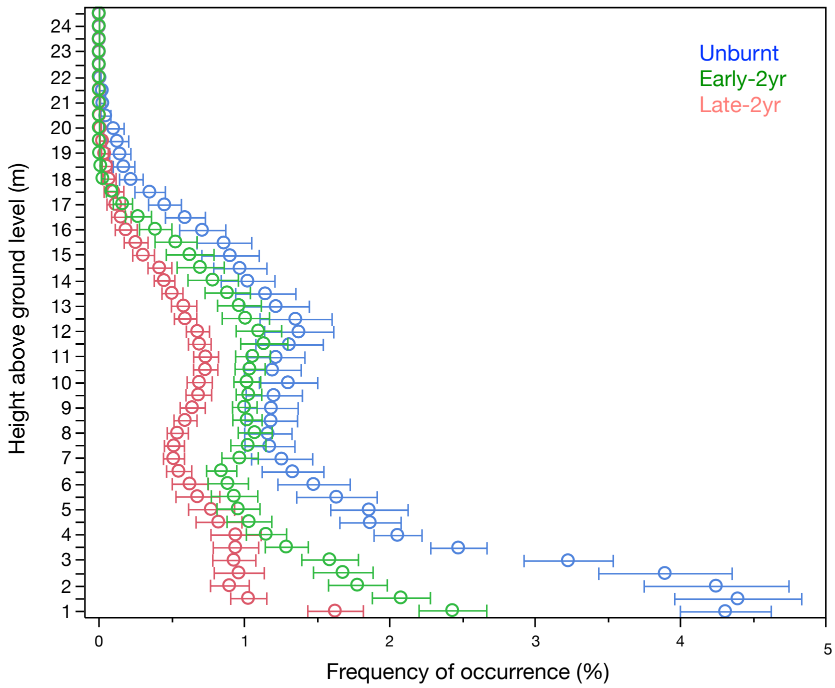

Figure 7. Effect of biennial fire season on woody vertical profile structure. Dots and error bars represent mean and standard error for the 30 m X 30 m subplots. 1 m tick on the y-axis represents the 1-2 m height class. Some returns from lower height classes may have arisen from herbaceous material.

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

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~~ that each fire regime generated a relatively unique niche space in ~~three-dimensions, and these~~ terms of vertical profile distribution. 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, these understorey height curves may represent stable persistent equilibrium resprout heights that define the ~~equilibrial size~~optimal 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 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 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 ~~valuable new insights into fire~~ 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 fire exclusion is rare in these tropical landscapes, so the starting ~~condition~~ 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). Furthermore, the rich 3D models that terrestrial LiDAR provide will open up new avenues for exploring actual 3D structural metrics.

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~~ 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 an ongoing fire regime experiment. Our results highlight the impact of late season burning on both carbon storage and on canopy vertical profile structure. Clear relationships between biodiversity and fire regimes have proven difficult to establish in savannas~~(and elsewhere). There have been~~ , despite many attempts at linking floral and faunal diversity directly to fire regime patterns~~, without explicitly accounting for associated vegetation structural heterogeneity~~. 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 ~~patterns~~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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