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Ecological implications of fine-scale fire patchiness and severity in tropical savannas of Northern Australia

Sofia L. J Oliveira
Universidade de Lisboa

Manuel L. Campagnolo
Universidade de Lisboa

Owen F. Price
University of Wollongong, oprice@uow.edu.au

Andrew C. Edwards
Charles Darwin University

Jeremy Russell-Smith
Charles Darwin University

See next page for additional authors

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Abstract

Understanding fine-scale fire patchiness has significant implications for ecological processes and biodiversity conservation. It can affect local extinction of and recolonisation by relatively immobile fauna and poorly seed-dispersed flora in fire-affected areas. This study assesses fine-scale fire patchiness and severity, and associated implications for biodiversity, in north Australian tropical savanna systems. We used line transects to sample burning patterns of ground layer vegetation in different seasons and vegetation structure types, within the perimeter of 35 fires that occurred between 2009 and 2011. We evaluated two main fire characteristics: patchiness (patch density and mean patch length) and severity (inferred from char and scorch heights, and char and ash proportions). The mean burned area of ground vegetation was 83% in the early dry season (EDS: May to July) and 93% in the late dry season (LDS: August to November). LDS fires were less patchy (smaller and fewer unburned patches), and had higher fire severity (higher mean char and scorch heights, and twice the proportion of ash) than EDS fires. Fire patchiness varied among vegetation types, declining under more open canopy structure. The relationship between burned area and fire severity depended on season, being strongly correlated in the EDS and uncorrelated in the LDS. Simulations performed to understand the implications of patchiness on the population dynamics of fire-interval sensitive plant species showed that small amounts of patchiness substantially enhance survival. Our results indicate that the ecological impacts of high frequency fires on fire-sensitive regional biodiversity elements are likely to be lower than has been predicted from remotely sensed studies that are based on assumptions of homogeneous burning.

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Sofia L. J Oliveira, Manuel L. Campagnolo, Owen F. Price, Andrew C. Edwards, Jeremy Russell-Smith, and Jose M. C Pereira

ECOLOGICAL IMPLICATIONS OF FINE-SCALE FIRE PATCHINESS AND SEVERITY IN TROPICAL SAVANNAS OF NORTHERN AUSTRALIA

Sofia L.J. Oliveira[1*], Manuel L. Campagnolo[1,2], Owen F. Price [3], Andrew C. Edwards [4], José M.C. Pereira[1], and Jeremy Russell-Smith[4]

[1] Centro de Estudos Florestais, Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisbon, Portugal

[2] Departamento de Ciências e Engenharia de Biossistemas, Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisbon, Portugal

[3] Institute for Conservation Biology and Environmental Management, University of Wollongong, New South Wales 2522, Australia

[4] Darwin Centre for Bushfire Research, RIEL, Charles Darwin University, Ellengowan Drive, Casuarina, Northern Territory 0810, Australia

[*] Corresponding author: Tel.: +351 213653387; e-mail:sofiaoliveiral@gmail.com

ABSTRACT

Understanding fine-scale fire patchiness has significant implications for ecological processes and biodiversity conservation. It can affect local extinction and recolonisation by relatively immobile fauna and poorly seed-dispersed flora in fire affected areas. This study assesses fine-scale fire patchiness and severity, and associated implications for biodiversity, in north Australian tropical savanna systems. We used line transects to sample burning patterns of ground layer vegetation in different seasons and vegetation structure types, within the perimeter of 35 fires, that occurred between 2009 and 2011. We evaluated two main fire characteristics: patchiness (patch density and mean patch length) and severity (inferred from char and scorch heights, and char and ash proportions). The mean burned area of ground vegetation was 83% in the early dry season (EDS: May-July) and 93% in the late dry season (LDS: August-November). LDS fires were less patchy (shorter and fewer unburned patches), and had higher fire severity (higher mean char and scorch heights, and twice the proportion of ash) than EDS fires. Fire patchiness varied among vegetation types, declining under more open canopy structure. The relationship between burned area and fire severity depended on season, being strongly correlated in the EDS and uncorrelated in the LDS. Simulations performed to understand the implications of patchiness on the population dynamics of fire interval-sensitive plant species showed that small amounts of patchiness substantially enhance survival. Our results indicate that the ecological impacts of high frequency fires on fire-sensitive regional biodiversity elements are likely to be lower than has been predicted based on assumptions of homogeneous burning derived from remotely sensed studies.

Keywords: biodiversity, fire patchiness, fire patterns, fire-sensitive plants, fire severity, northern Australia savannas, season, unburned patch, vegetation communities.

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INTRODUCTION

North Australian tropical savannas cover 1.9 M km^2 and are among the most fire-prone ecosystems in the world. Over that vast region, annual fire frequencies range from over 50% in higher rainfall regions to <5% in heavily grazed semi-arid savanna regions, with an overall mean frequency of 19%, over the period 1997–2005 (Russell-Smith *et al.* 2007). In these ecosystems, fire is a natural ecological process required for maintaining biological diversity (Russell-Smith *et al.* 2002*a*, Bowman *et al.* 2003). Fire patchiness is an important ecological component of savanna fire regimes because unburned patches can influence a variety of processes, including local extinction of and recolonisation by relative immobile fauna and poorly seed-dispersed flora (Prada 2001, Russell-Smith *et al.* 2002*b*, Gill *et al.* 2003, Parr and Chown 2003, Price *et al.* 2003). While little studied, understanding fire patchiness has significant implications for biodiversity conservation and ecologically sustainable fire management in fire-probe systems (Bradstock *et al.* 1998, Ooi *et al.* 2006, Parr and Andersen 2006, Driscoll *et al.* 2010).

In general, a patch can be defined as a set of contiguous, adjacent observations of the same attribute (Turner 1990) and is therefore dependent on the scale of observations. This study focused on the distribution of burned and unburned ground layer patches contained within fire perimeters; that is, within the entire outer edge or boundary of a fire. The distribution of unburned patches within a burned area can be deterministic, attributed to a landscape condition (e.g. heterogeneity of fuel type, topography, drainage lines), fire-behaviour, weather, or it may be stochastic, regarded as being caused by chance, if their place of occurrence in successive fires is unpredictable (Gill *et al.* 2003). These unburned patches provide refuge for relatively immobile animals and fire- sensitive plants, becoming an important source for the propagation of seeds, especially when an area is burnt so frequently that local extinction of obligate-seeder plant species can occur (Bradstock *et al.* 1998, Edwards *et al.* 2001, Burrows and Wardell-Johnson 2003, Panzer 2003). Fire patchiness also has implications for watershed hydrology, soil stability, and may be applied strategically to reduce the risk of hazardous wildfires (Bradstock *et al.* 1998).

Prior to European colonisation, indigenous (Aboriginal) people managed north Australian savanna landscapes with fire, commencing burning in the early part of the dry season, (EDS; May-July) and producing highly patchy fires (Russell-Smith 1995, Yibarbuk *et al.* 2001, Garde *et al.* 2009). Traditional burning was, however, progressively abandoned throughout most of northern Australia as a consequence of European colonisation. Contemporary fire regimes are characterised by frequent, extensive and homogeneous, anthropogenic fires occurring mostly in the late dry season (LDS; August–November), under severe fire-climate conditions (Gill *et al.* 1996). Such fire regimes are also the source of significant emissions of accountable greenhouse gases, and annually represent 2% to 4% of Australia's National Greenhouse Gas Inventory (AGO 2013). In northern Australia, contemporary fire regimes and associated reduction in fire patchiness are implicated in population declines of a range of obligate-seeder taxa, including the native cypress *Callitris intratropica* (Bowman and Panton 1993) and the endemic myrtaceous shrub *Petraeomyrtus punicea* (Russell-Smith *et al.* 2002*a*), granivorous birds (Franklin 1999) and small mammals (Braithwaite 1995, Woinarski *et al.* 2001, Price *et al.* 2005).

Various studies have been undertaken to better understand fire patchiness, for a variety of ecological and associated land management purposes, in the USA (Turner *et al.* 1994, Slocum *et al.* 2003), southern Africa (Hudak *et al.* 2004) , Spain (Román-Cuesta *et al.* 2009) and Australia (Russell-Smith *et al.* 1997, Allan 2001, Russell-Smith *et al.* 2002*b*, Russell-Smith and Edwards 2006). Russell-Smith and Edwards (2006) reported that EDS fires have 80% probability of being of low severity and would therefore be expected to have greater internal patchiness than LDS fires. In semi-arid savannas, Allan (2001) reported that EDS fires had more internal area unburned (14.8%) compared with LDS fires (8.5%). Price *et al.* (2003) assessed fine-scale patchiness through field measurements in northern Australia and stated that a key issue with the above studies is that the scale of most remotely sensed imagery used, predominantly from the MODIS and Landsat sensors, cannot detect fine-scale patches (≈1m scale). Although the importance of fire patchiness has been widely questioned and recognised, evidence regarding its ecological significance is largely anecdotal (Bradstock *et al.* 1996, Ooi *et al.* 2006, Parr and Andersen 2006).

The aim of this study is to describe fine-scale fire patchiness and severity in northern Australia savannas, by season and savanna vegetation type, and how patchiness is likely to affect the demography of fire interval-sensitive (obligate seeder) plants. The following hypotheses were tested: i) burned area and fire severity are highest, and patchiness lowest, in the LDS; ii) patchiness and burned area differ by vegetation structure type; iii) percentage area burned is a scale-dependent function of fire severity; iv) plant survival increases with fire patchiness.

DATA AND METHODS

Data collection and study areas

We used line transects to assess fire patchiness along recently burned areas, covering five different vegetation structure types that correspond broadly to the types defined in Edwards and Russell-Smith (2009): open forests (OF) dominated by tall *Eucalyptus spp.* (8-20m) with FPC >30%, developed on well drained deeper sands, over a range of shrubs and slender perennial and annual grasses; woodlands (WD), typically dominated by *Eucalyptus tetrodonta* and *E. miniata*, with ≤ 30% foliage projected cover (FPC), over an understory of perennial and annual grasses; open woodlands (OWD), also dominated by *E. tetrodonta* and *E. miniata,* with ≤ 10% FPC; sandstone woodlands (SWD), with FPC <30%, dominated by

Eucalyptus spp. with well-developed shrub layers and a mixture of native perennial and annual tussock and hummock (*Triodia*) grasses, occurring on shallow to rocky soils also derived from sandstone and sandstone heaths (SH), with FPC ranging from 10-30%, typically comprising a diverse range of shrubs and occasional small trees over a diverse herbaceous ground layer dominated by perennial hummock (*Triodia*) grasses, and occupying rugged, dissected substrates derived from sandstone.

The burned surveyed areas are all located in the Northern Territory, where the climate is defined by wet and dry seasons with 90% of the annual rainfall occurring in the wet season months of December to April, and an average annual rainfall between 2000mm and 500mm along a north-south gradient (Australian Bureau of Meteorology 2013). All the areas sampled burned between 2009 and 2011, either in the EDS or in the LDS (Appendix 1). The distribution of 68 study locations is given in Fig. 1.

The starting point and direction of each transect was randomly selected within the boundary of the fire, and a footfall method was used: with the observer walking along the selected bearing and for every footfall (at ≈1m intervals) recording whether the ground immediately in front of the toe of the shoe was burned or unburned. Where the sample point was burned, it was recorded whether the surface was covered with char, ash, vegetation (photosynthetic or non-photosynthetic vegetation, i.e., green vegetative material or dry grass, dead leaves, stems and twigs), and bare soil or rock. If the sample point was unburned the presence of vegetation, and bare soil or rock was recorded (Table 1). Typically, a burned point contained burned vegetation, ash or bare soil/rock, while an unburned point comprised a live plant or unburned litter. Every 50 steps (≈50m), we recorded average char and scorch heights by visual estimation, over the entire 50m. Char height was recorded as the height above ground of blackened (burnt) fire-affected material. Scorch height was recorded as the height above ground of heat affected (scorched) foliage. We used the field database

CyberTracker (www.cybertracker.org.), installed on a handheld computer, to record observations and an associated GPS location for each sample point. These were plotted in ArcGIS to determine transect length, and to calculate the mean footfall distance (1.062m) which was assumed to be the constant inter-point distance in subsequent analysis.

Data analysis

Each transect was described by season, vegetation type, number of sampled footfall points, field measurements and additional variables derived from the field data (% burned, patch density, and mean patch length) (Table 1). Percentage burned was calculated by dividing the number of burned points by the total number of points on a transect. Patch density, the number of unburned patches (km^{-1}), was obtained by counting the number of patches (contiguous unburned footfall points) on a transect, and dividing this by the total length of the transect. Mean patch length was obtained by averaging the length of unburned patches. Patch density and mean patch length were used for assessments of fire patchiness; char height, scorch height, and mean percentage of char and ash were used for assessments of fire severity.

Data were analyzed both by season and vegetation type. To assess the data only by season, all transects were considered (n=68). To assess the data by vegetation structure type and season, transects containing more than one vegetation type were partitioned into separate transects; for example, a transect encompassing three different vegetation types was divided into three transects. This partitioning resulted in a total of 79 transect units.

Field measurements and derived variables were compared for seasonal and vegetation type differences, using analysis of variance (ANOVA). Before performing ANOVA, the normality and homogeneity of variances of the data were tested using the Shapiro-Wilk and the Bartlett tests, respectively.

Regression analysis of fire severity metrics. Regression analysis was used to assess the existence of a relationship between fire severity and percentage area burned. Char and scorch heights were used as indicators of fire severity, because they are strongly related to fire intensity in northern Australia (Williams *et al.* 2003), and with fire severity (Keeley 2009, Edwards *et al.* 2013). Specifically, regression analyses were performed for char height vs. scorch height, char height vs. % burned, and scorch height vs. % burned. The initial char and scorch height data, collected every 50m, were aggregated at different levels (100m, 150m, and 250) to assess the effects of spatial scale. The highest level of aggregation was kept at 200m in order not to eliminate data, since several transect units were around 200m in length.

Simulation of plant population dynamics. Implications of patchiness on the population viability of fire interval-sensitive (obligate seeder) plants was investigated via a simulation analysis whereby a population of plants which is killed by fire but can establish from seed after firewas subject to a fire regime with different fixed levels of patchiness. For modeling purposes we assumed that reproductive maturity of our hypothethical species could be attained after seven years based on observations for *Callitris intratropica*, a common coniferous tree in regional savannas (Bowman and Panton 1993) and *Petraeomyrtus punicea,* a regionally endemic myrtaceous shrub (Russell-Smith 2006). At the start of the simulation there were 1000 locations each occupied by a plant. Each plant was considered independently. The chance that it burned in each year was the product of the probability of a fire occurring (set at 0.3 for all simulations to reflect typical savanna fire return intervals under higher rainfall conditions; e.g. Russell-Smith *et al.* 2007) and the percentage burned by the fire, which was set as one of four levels (50, 83, 93 or 100). The 83% and 93% values reflect levels of the burned area in EDS and LDS fires found in this study, and the bounding

50% and 100% values are used for comparisons. A random number drawn from a lognormal distribution (as described in Oliveira *et al.* 2013) was used to determine whether a location burnt in any one year. A burnt location could be re-populated (probability R) if there were no fires for seven subsequent years (to reflect the life cycle of above obligate seeder taxa), determined by a random number proportional to the overall population size (R=N/500 if N<500 and R=1 if N>=500). The simulation was run for 100 years.

RESULTS

Field transects

The number and length of surveyed line transects is presented in Table 2, grouped according to season and vegetation structure type. Thirty four transects were surveyed separately in both the EDS and LDS. There were fewer SH and SWD transects due to accessibility limitations. The profiles of unburned points for each transect are shown in Fig. 2.

Comparison of burnt transects by season. The mean percentage burned within fire perimeters was higher in the LDS (93%; SEM=1.5) compared to the EDS (83%; SEM=1.7) (Fig. 3a). At least 54% of the ground vegetation was burnt in all transects. In the EDS only one transect was burnt completely while in the LDS 10 transects were completely burnt. The percentage of exposed rock and bare soil was higher in transects sampled in the LDS (Fig. 3b). Relative proportions of char and ash were dependent on season: mean % ash was twice as high in the LDS (12%) than in the EDS (6%) and mean % char was lower in the LDS (59%) compared to the EDS (65%). Ash indicates near-complete combustion of the fuel while char indicates incomplete combustion, which corroborates the higher fire severity pattern in the LDS than in the EDS. Both char height and scorch height were higher in the

LDS (Fig. 3c). The mean char and scorch heights were higher (1.4m and 7.2m, respectively) for transects that burned completely in the LDS than the mean values for all LDS transects. This observation reinforces the idea that there is a quantitative relationship between char/scorch heights and burned area. Unburned patch density and mean unburned patch length were higher in the EDS than in the LDS (Fig. 3d,e). The majority of unburned patches (51%) corresponded to a single observation (≈1m). Small patches (1m) were considerably more common in the EDS (Fig. 4) and large patches (≥ 20m) were also more abundant in the EDS. A large percentage of patches (87% in the EDS and 89% in the LDS) were ≤ 5m and only a small percentage of patches were ≥ 20m (3% in the EDS and 2% in the LDS).

Comparison of burnt transects by season and vegetation structure type. When considering the partitioned transects by vegetation type, the same overall seasonal trends described for fire transects by season were observed (Appendix 2). Burned area was also lowest in the EDS and patch density and mean patch length were highest in the EDS, for almost all vegetation types. Open woodlands (OWD) were the most extensively burnt vegetation type and SWD the least. Mean char and scorch heights were highest in OWD in the EDS, and in WD in the LDS. Patch density was highest in SH and lowest in OWD. Mean unburned patch length was almost five times higher in OF when compared to the lowest value, observed in OWD.

Statistical comparison by season and vegetation structure type

There was no evidence to reject the assumption of normality of the data and the homogeneity of variances. The p-values of the two-factor ANOVA tests are displayed in Table 3. The results suggest that % burned, % char, % ash, and patch density differed by season; % char, % ash, and patch density differed by vegetation type; and, significant interaction effects between season and vegetation type were observed for % char, % ash, scorch height, and char height.

Regression analysis of fire severity measures

The level of data aggregation that produced the strongest correlation between char and scorch heights was 200m. There was a weak positive correlation between these two variables in the EDS (R^2= 0.30) and a stronger correlation in the LDS (R^2= 0.66); the regressions were significant at the 0.01% level (p=0.000 and p= 0.000, respectively). The correlations with data aggregated at 50m, 100m, and 150m were respectively R^2= 0.28, 0.29, and 0.34 in the EDS and R^2= 0.43, 0.51, and 0.49 in the LDS; all regressions were significant at the 5% level (p<0.000).

When assessing the relationship between scorch height and % burned area, the best results were also obtained when aggregating data at 200m. The relationship between the two variables was approximately logarithmic (Fig. 5). Seventy percent of the EDS burned area variability is explained by mean scorch height (Fig. 5a) but no relationship was found for the LDS (Fig. 5b). The correlations with data aggregated at 50m, 100m, and 150m were approximately R^2= 0 in the LDS and R^2=0.23, 0.39, and 0.59 in the EDS, respectively. The relationship between char height and burned area was always lowest (Fig. 5c, d), than that between scorch height and burned area, but the same trends remain, with the best relationship between the two variables in the EDS. The correlations with data aggregated at 50m, 100m, and 150m were approximately R^2= 0 in the LDS and R^2=0.19, 0.23, and 0.40 in the EDS, respectively. Usually, completely burned transects have higher values for char and scorch heights than partially burned transects.

Simulation of plant population dynamics

Plant population simulation results suggested that the higher the patchiness, the greater the number of surviving obligate seeding plants. The plants became extinct after 22 years when there was no patchiness, or after 40 years with 93% burnt (mean burned area of LDS transects) (Fig. 6). The population persisted for at least 100 years with higher levels of patchiness, with a mean remnant population of 19 plants with 83% burned (mean burned area of EDS transects) and 284 with 50% burned. When the simulations were repeated without the ability to repopulate, extinction occurred in all scenarios, but the time taken to extinction increased with patchiness.

DISCUSSION

This study extends the findings of previous work on fire patchiness in tropical savannas of northern Australia (e.g. Price *et al.* 2003, Russell-Smith *et al.* 2003, Williams *et al.* 2003). We found that seasonality is the factor that most influences percent area burned and fire severity, and that patchiness, mainly patch density, is strongly influenced by vegetation structure type, possibly due to variation in fuel continuity. Fire severity is also influenced by the interaction between season and vegetation structure type.

Late dry season fires tend to burn over more area and, in this study, were found to be more severe and less patchy (shorter and fewer frequent unburned patches) than EDS fires, which is congruent with other Australian and worldwide studies (e.g. Allan 2001, Slocum *et al.* 2003, Russell-Smith and Edwards 2006). Grasses, the dominant component of the combustible fuel in these savannas, progressively cure and collapse with the onset of the dry season. In addition, relative humidity and soil moisture decrease, whereas temperature and wind speed increase (Gill *et al.* 1996), creating ideal conditions for fire spread. The internal unburned percentage recorded in this study (17% for the EDS and 7% for the LDS) was very similar to the results obtained by Allan (2001) for a semi-arid savanna in northern Australia (15% for the EDS and 8.5% for the LDS). Our LDS values are also similar to those given in Russell-Smith *et al.* (2003). However, compared to the study of Price *et al.* (2003), the fires studied here had lower patchiness and the patches were generally much smaller.

Much of the patchiness described in Price *et al.* (2003) was due to rockiness, and most of the transects (including all of the LDS fires) were in rocky areas. Rockiness is known to strongly influence patchiness (Price *et al.* 2003). In this study, the mean percentage of rock was 2% and, accounting for bare soil, the percentage increased to 16%, a value much lower than the 39% reported by Price *et al.* (2003) for mean rockiness. Another reason for the disparity in results may be the fact that Price *et al.* (2003) included some fires or parts of fires from both seasons where intensity was very low. Likewise, for prescribed burns in southern Australian eucalypt forests, Penman *et al.* (2007) reported greater patchiness than observed here, with burned area values ranging from 10% to 100%, with a mean of 65%. By contrast, in this study, open forest burned area ranged from 77% in the EDS to 93% in the LDS. There are several likely reasons for this: prescribed burns are typically of low intensity, fire intensities of fuel reduction burns are higher in northern Australia compared to southern Australia (Williams *et al.* 1998), and differences in fuel type and architecture influence fire behaviour.

Patchiness (patch density and mean patch length) was lowest in OWD, which was also the vegetation structure type with the highest percent burned (in agreement with Russell-Smith *et al.* 2003). According to Cheney and Sullivan (2008), fuel continuity, the extent to which the surface of the ground is covered by fuel, is the main characteristic influencing fire spread. Open woodlands (OWD) are dominated by flammable tall annual sorghum and perennial grasses, supplemented by scattered leaf litter that can fill bare patches in the grass sward, making for a more continuous fuel bed. On the other hand, percent burned was lowest in sandstone types and patch frequency was highest, due to decreased fuel continuity caused by a large proportion of exposed rock surfaces. Rocky surfaces and bare soil act as barriers to fire spread and discontinuous grasslands will not carry a fire until the wind speed exceeds a particular threshold (Cheney and Sullivan 2008).

Open forests exhibited the longest mean patches, possibly due to greater fuel moisture content, associated with the highest percent canopy cover of all vegetation types. Moisture content has a major effect on fire spread; fires typically will not spread when grasslands are ≤50% cured, and only reach their full fire spread potential when they are >95% cured (Cheney and Sullivan 2008).

There was a strong relationship between char and scorch heights in the LDS, mostly because of the influence of very high values of scorch height and because there is much less charred material to assess in the lower severity char heights in the EDS. Burned area and severity were strongly correlated in the EDS, with 70% of burned area explained by mean scorch height. In the LDS, the percentage burned was very high (close to 100%) across a wide range of scorch height values, which explains the weak relationship between the two variables. There is an improvement in the relationship between these variables with spatial aggregation given that variance is reduced by data smoothing. By aggregating the data (initially collected every 50m) up to 200m, disparate observations are diluted, confirming the scale dependence of this relationship.

In this study scorch height was found to be a better surrogate of fire severity than char height, being better related to percent area burned than char height. Some authors recommend that measurements of fire severity should be restricted to measures of organic matter loss, such as canopy scorch or ash deposition (e.g. Keeley 2009), which is potentially what one is measuring with scorch height in tropical savanna habitats dominated with ground fires, given little or no canopy fire spread. Char height may not always be closely correlated with flame length (and thus, fire severity), given localised variation in wind and variation in the size and moisture content of leaves (Williams *et al.* 2003), but also due to the paucity of vegetation between ground and upper strata. White ash is also an important indicator of fire severity (Edwards *et al.* 2013). It has been positively correlated with fire intensity and represents near-complete combustion of the available fuel, offering little protection to the soil from rainfall and therefore erosion (Roy *et al.* 2010). The increased % ash in the LDS (twice as high) confirms the greater severity of the LDS fires. Charred vegetation is typically conspicuous in the EDS, associated with variable, low severity fires.

An important observation of this study is that obligate seeder survival simulations are sensitive to small differences in fire patchiness, such as the 10% difference observed between the EDS and the LDS. *Petraeomyrtus punicea* seed fall is limited to the near vicinity of adult canopies, with secondary transport downslope (Russell-Smith 2006), so small patches (<5m), like the ones observed in this study, are very important for plant reproduction. *Callitris intratropica* seedlings can survive a fire if only partially scorched or, in cases of low severity fires even if totally scorched (Russell-Smith 2006). Thus, even though most unburned patches were <5 m wide, they provide an important refuge for fire-sensitive plants. It follows that small and relative immobile fauna likewise can find refuge in such patches, whether in holes, crevices, under rocks or in above-ground shrub foliage and tree hollows.

These findings support arguments advanced by many authors concerning the regional biodiversity benefits of smaller, patchier EDS savanna fires (e.g. Edwards *et al.* 2001; Russell-smith *et al.* 2002*b*, 2003; Andersen *et al.* 2005; Yates *et al.* 2008). Many studies have also argued that implementing a prescribed EDS burning program has substantial benefits in restricting the spread of extensive LDS wildfires (e.g. Russell-Smith *et al.* 1997, 2003; Yates *et al.* 2008; Price *et al.* 2012). For example, by imposing prescribed EDS burning between 2005-2009 over 24,000 km^2 in western Arnhem Land, Price *et al.* (2012) showed that mean fire extent in the LDS period was reduced by 16.5% by comparison with the mean extent for the prior 15 years, yielding a mean overall reduction of 6%. Reduction in the extent and severity of LDS fires is known to have significant benefits both for obligate seeders and resprouting species (Williams *et al.* 1998, 1999; Russell-Smith *et al.* 2002*b*, 2012).

A considerable challenge for biodiversity management is to better understand and deliver spatio-temporal fire patchiness, especially in relation to rapid accumulation of grassy fuels. Another approach for biodiversity management should be increasing both the spatial heterogeneity and non-randomness of EDS burning through strategic application of prescribed burning (e.g. using streams and tracks as fire-breaks), so that patches of long-unburned vegetation are more effectively compartmentalised, reducing the potential for large, severe fires (Turner *et al.* 1994, Andersen *et al.* 2005).

CONCLUSION

Currently available, systematically acquired remote sensing data are inadequate to study fire patterns at a spatial scale relevant to individuals and populations of plants, and lack the spatial resolution to account for the fine-scale patchiness that is associated with fire scars, especially in more patchy EDS fires. For this reason, in-situ transects were used in this study to detect and describe fire patterns at a finer spatial scale (≈1m) than in previous studies.

We found that seasonal timing of fires affected burned area, vegetation structural type influenced fire patchiness, and the interaction between season and vegetation type affected fire severity. All initial hypotheses were supported: i) burned area and fire severity were higher in the LDS and patchiness lower (shorter and less frequent unburned patches) than in the EDS; ii) patchiness differed by vegetation structure type, with sandstone heaths having the highest patch frequency (low fuel continuity due to larger proportion of exposed rock surfaces), OWD the lowest (associated with greater continuity of grassy fuels), OF had the longest mean patches (associated with highest canopy cover and possibly greater fuel moisture content; iii) fire severity and percentage area burned were strongly related in the EDS, with 70% of EDS burned area being explained by mean scorch height with the relationship between these two variables increasing with spatial aggregation of the data, given that extreme data values were smoothed; and most importantly from a biodiversity conservation perspective, iv) increasing fire patchiness was shown to substantially enhance the survival of fire-sensitive (obligate seeder) species even at small unburnt patch sizes.

The risk of localized extinction of fire-sensitive obligate seeders may be reduced with the use of prescribed burning undertaken in the EDS through increased fire patchiness and reduced severity. In this study, almost all fires surveyed contained unburned patches, although most of these were very small (<5m). These results suggest that the ecological impacts of high frequency fires are likely to be lower than has been predicted based on assumptions of homogeneous burning derived from remotely sensed studies; there was almost always some chance that fire-sensitive species could survive a fire, and this chance increases in rockier habitats which contain the greater proportion of regional endemics.

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FIGURE CAPTIONS

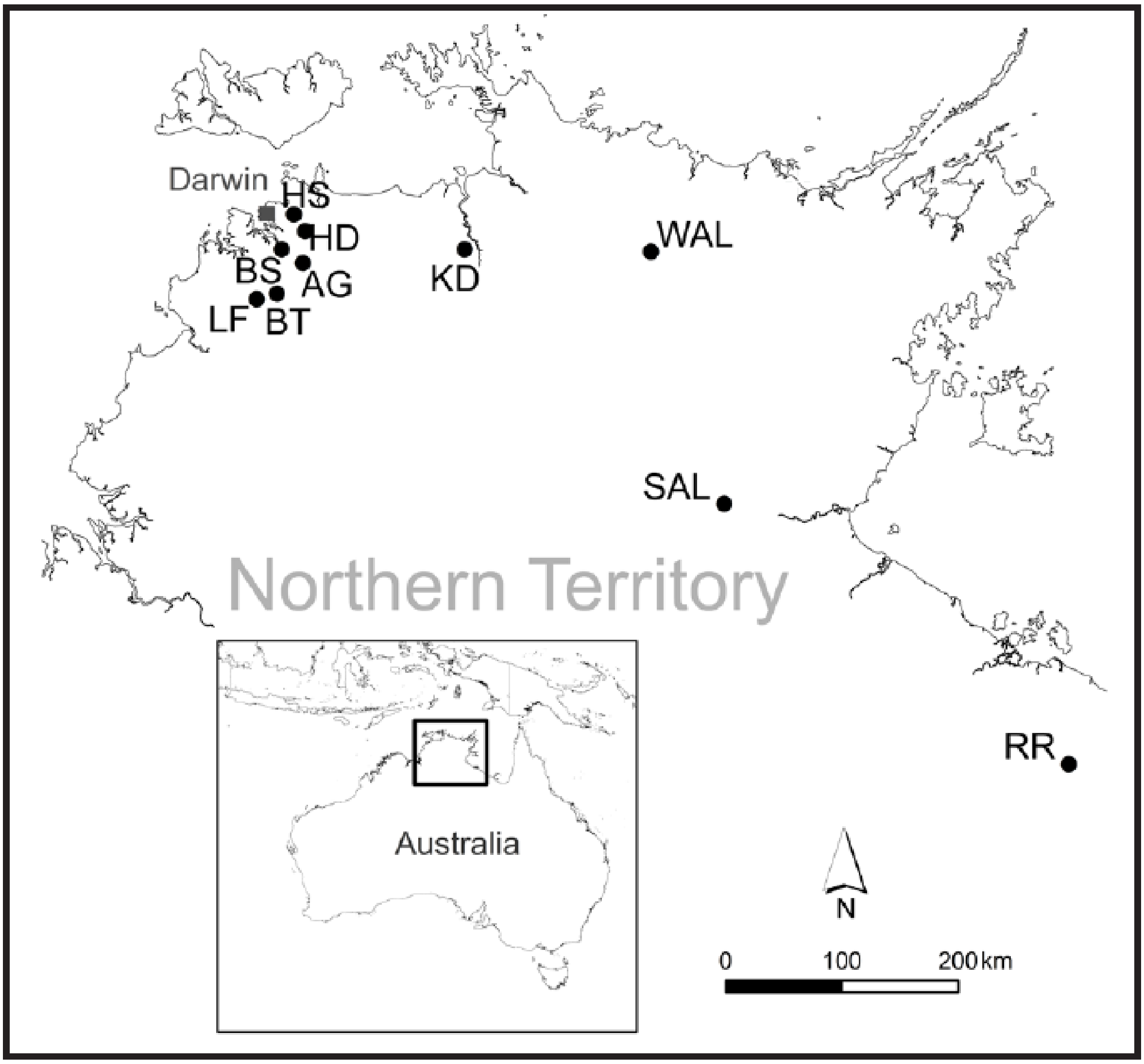

Fig. 1. Location of the study areas in the Northern Territory, Australia.

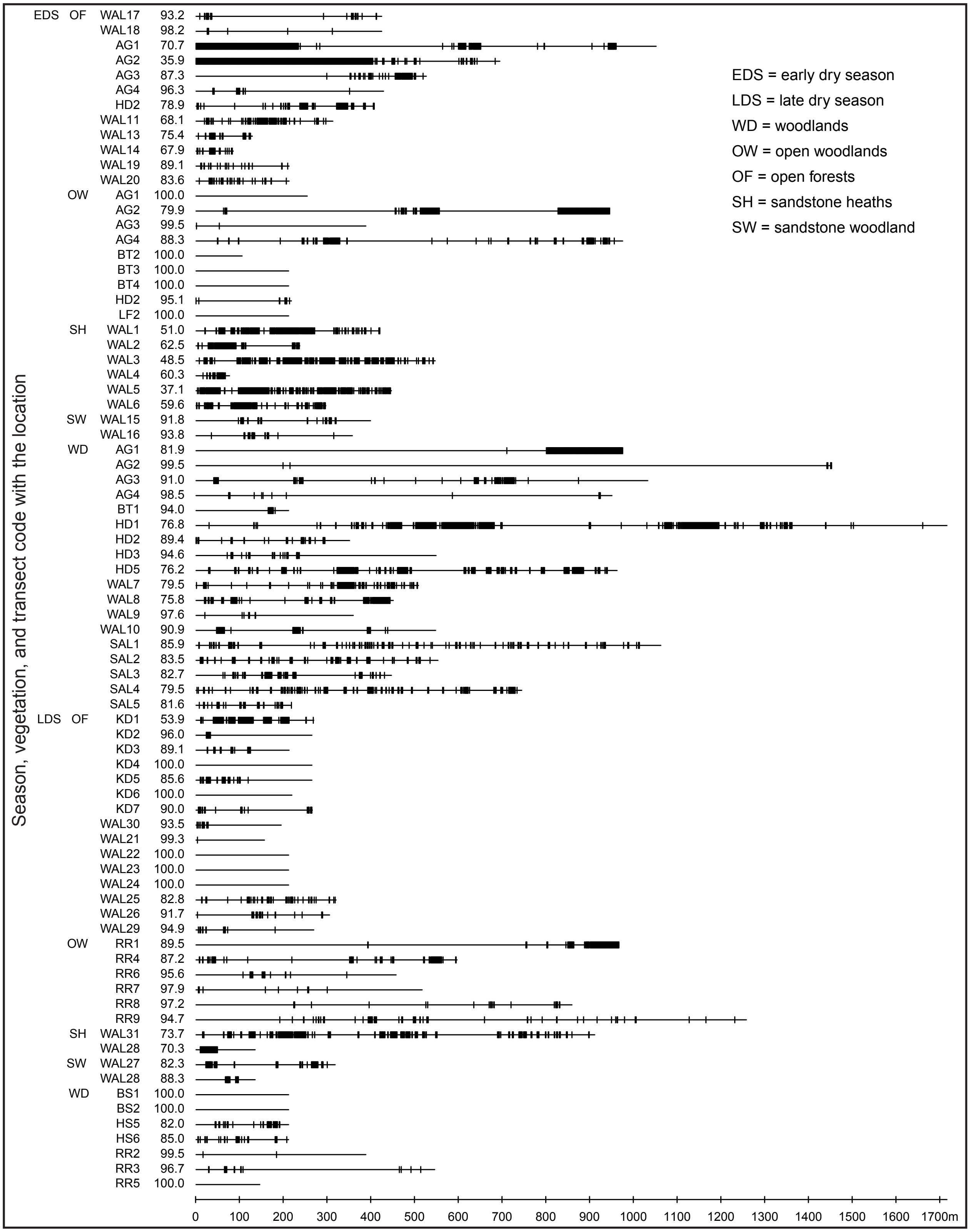

Figure 2. Transect profiles of unburned points (black vertical lines) grouped by season and vegetation type. Each transect containing more than one vegetation type was segmented by vegetation type, and for two-way ANOVA only its longest segment was kept. Next to each transect is the percentage of the transect that burned.

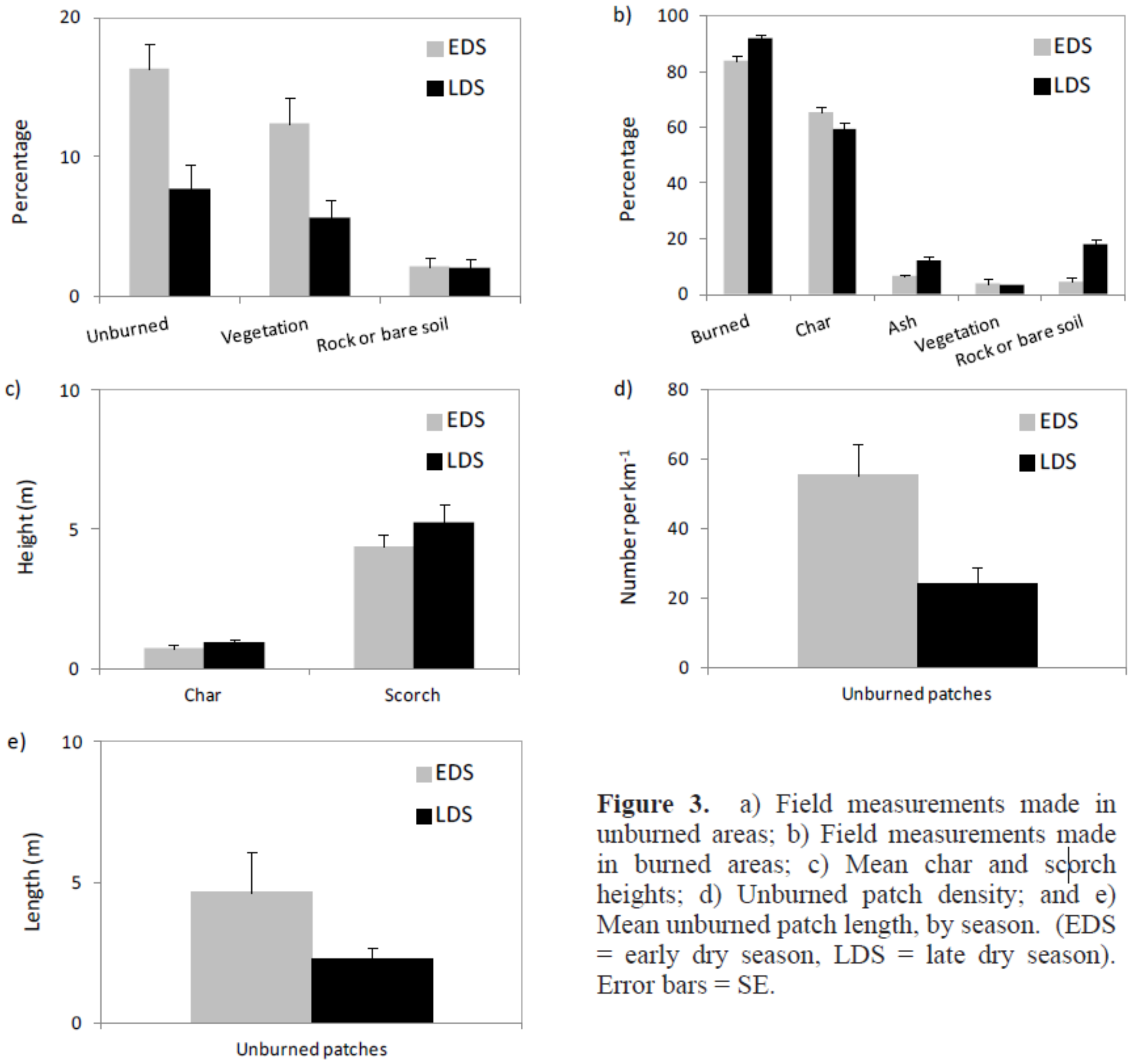

Figure 3. a) Field measurements made in unburned areas; b) Field measurements made in burned areas; c) Mean char and scorch heights; d) Unburned patch density; and e) Mean unburned patch length, by season. (EDS = early dry season, LDS = late dry season). Error bars = SE.

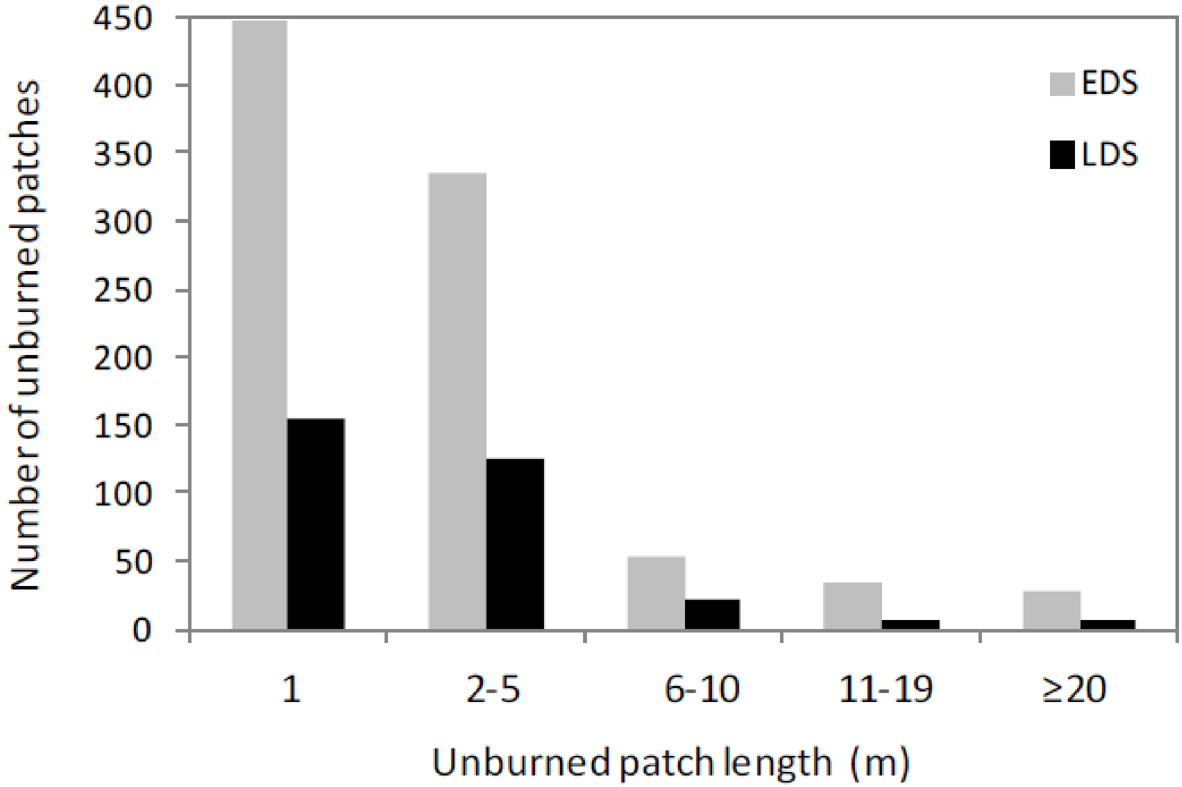

Fig. 4. Frequency distribution of unburned patch size for the early dry season (EDS) and late dry season (LDS).

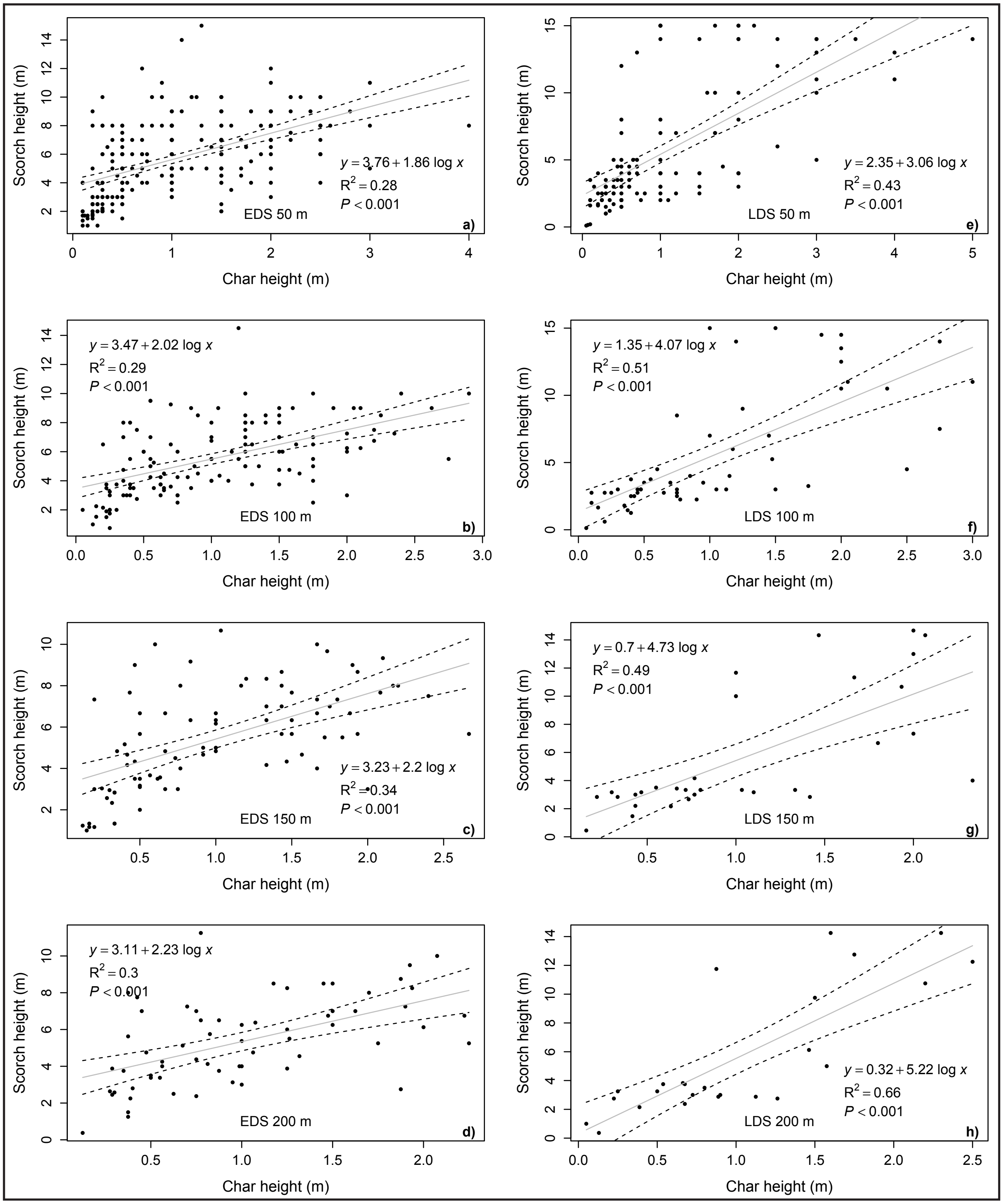

Figure 5. Regression analysis between char and scorch heights in the early dry season (EDS) for data aggregated at a) 50 m, b) 100 m, c) 150 m, and d) 200 m, and in the late dry season (LDS) for data aggregated at e) 50 m, f) 100 m, g) 150 m, and h) 200 m. Dashed lines correspond to a 95% confidence band around the regression line.

TABLES

Table 1. Field data collected along transects and derived variables.

Measurement frequency	Fire class	Field measurements and derived variables
≈1 m	Burned	Char (yes/no) Ash (yes/no) Vegetation (yes/no) Rock or bare soil (yes/no)
	Unburned	Vegetation (yes/no) Rock or bare soil (yes/no)
≈50 m		Char height (m) Scorch height (m)
Transect		Patch Density (km^{-1}) Mean patch length (m)

Table 2. Summary of seasonality and vegetation structure characteristics of surveyed transects. Season refers to the seasonality of the original transects, and Season x Vegetation refers to transects partitioned by vegetation structure type and season. (EDS=Early dry season, LDS=Late Dry Season, OF= open forests; WD=woodlands, OWD= open woodlands; SWD= sandstone woodlands SH= sandstone heaths).

	Season	Vegetation	No. of transects	Total No. of transects	Length (m)	Total Length (m)
Season	EDS		34	68	23710	38159
	LDS		34		14450	
Season x Vegetation	EDS	OF	12	79	495113092	
		WD	18		130922889	
		OWD	9		28894951	
		SWD	2		7572020	
		SH	6		2020757	
	LDS	OFWD	157		36764469	
		WDOWD	76		44694799	
		OWDOF	615		47993676	
		SWDSH	2		4551051	
		SHSWD	2		1051455	

Table 3. Significant p-values for the ANOVA.

	p-values		
	Season	**Vegetation**	**Season x vegetation**
Percentage burned	0.0037	-	-
Percentage char	0.0378	0.0254	0.0174
Percentage ash	0.0013	0.0092	0.0169
Scorch height	-	-	0.0225
Char height	-	-	0.0438
Patch density	0.0017	0.0106	-
Patch length	-	-	-