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Three decades of monitoring the woody layer of tropical eucalypt woodlands of northern Queensland

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Abstract: Thirty years of vegetation monitoring data in the eastern savannas of Australia provides some insights into the temporal dynamics of woodlands at these sites, and supplements long-term savanna studies in the Northern Territory. Across four sites in four ecosystems, there was an increase in native shrub species abundance consequent with a decrease of canopy species abundance in the low tree and canopy layers. Even though some individuals from a variety of species persisted through at least six fires, with three developing to be low subcanopy trees, there were no individuals that survived to become canopy trees. The loss of canopy trees with no replacement and recent increase in the non-native shrub *Stylosanthes scabra* may indicate an ecosystem under stress leading to long-term changes in structure and species composition at these sites.

Keywords: species turnover, floristic diversity, vegetation, savannas, sampling, woodlands

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Introduction

The tropical savannas in Australia are one of the most widespread landscape patterns and cover a large proportion of northern Australia (Fox *et al.* 2001). This includes much of continental Australia north of a line between Rockhampton on the east coast, and Broome on the west coast (Fig. 1). As in tropical savannas in other parts of the world, water availability and soil nutrients are primary determinants of the resultant vegetation (Scholes & Archer 1997). The Australian tropical savannas occur within three major rainfall zones; the semi-arid zone which receives 250-500 mm rainfall annually, semi-humid which receives 500-1000 mm rainfall and the humid zone which receives greater than 1000 mm annually (Fox *et al.* 2001). This precipitation falls predominantly during the summer wet season (November-April) with very little precipitation during the winter dry season. Mesic savannas where annual precipitation is greater than 650 mm are the most frequently burned biome in the world (Chuvieco *et al.* 2008). However, fire and grazing which are frequently used by humans as management tools are secondary determinants of the extant vegetation (Bond & Van Wilgen 1996; Walker *et al.* 1981). Savanna dynamics have been the subject of long-term monitoring internationally, including noteworthy examples from the Northern Territory in tropical Australia, Munmarlary experiment 1973 to 1996, and Kapalga from 1989 to 1995 (Bowman *et al.*1988, Bowman & Panton 1995, Williams *et al.* 2003b), and the Northern Australia Tropical Transect and Three Parks vegetation and fire monitoring program (Russell-Smith 2013). These studies have focused on the dynamics of woody trees and shrubs and their responses to fire and herbivory (Williams *et al*. 2003a, Midgley *et al.* 2010), however there are few monitoring studies in the tropical savannas of Queensland.

Australian savanna vegetation comprises open wooded grassy landscapes in which a flush of annual flora, including many forbs, appears after the summer rains and persists only briefly before senescence (Wilson *et al.* 1990, Fox et al. 2001). The tall grasses, which proliferate during the wet season, are usually burnt off during the dry season (Allan *et al.* 2001, Williams *et al.* 1999). Fires, which are deliberately lit by either First Nations peoples, pastoralists or forest managers, or naturally lit by lightning strikes, can greatly impact on the plant species recorded when sampling tropical savanna vegetation, with most of ground layer burnt in most fires.

Murphy *et al.* (2015) in their review of the literature regarding the role of fire on biomass in Australian savannas conclude that the Australian savannas may behave differently from savannas in South America and Africa because of the extremely fire-resistant dominant trees – the eucalypts (Bond *et al.* 2012). They propose that the well supported fire trap conceptual model, while applying to broad leaved more mesic species, is not the primary mechanism for controlling recruitment and biomass in the dominant canopy trees in Australian savannas. Instead, water availability particularly through the long dry season and competition for this water and potentially also nutrients between canopy trees and the understory may be more influential on recruitment and stand structure than fire frequency and intensity (Murphy *et al.* 2015). Studies from the monsoonal eucalypt savanna highlight the importance of competition as a mechanism inhibiting small trees from advancing to the sapling layer (Fensham & Bowman, 1992, Prior *et al.*, 2006, Russell-Smith *et al.* 2019). In mesic savannas, the ground layer has the potential to compete with trees of all sizes for nutrients and water as shown in African, Australian and North American savannas (Menaut *et al.* 1990, Prior *et al.* 2006, Archer 1995). The amount and type of ground layer may impact on the degree of competition with the juvenile trees. Werner & Prior (2013) contrast the competition for nutrients between an annual sorghum ground layer and a perennial grass layer and illustrate that this also interacts with the fire behaviour with different ground layers.

Severe drought periods such as 1991-1994 in north-eastern Queensland have resulted in reductions in live tree basal areas of an average of 29% across 195 sites (Fensham & Holman 1999). In the monsoonal savanna of northern Australia, in areas not supporting a high biomass of invasive grasses, a range of fire regimes has a relatively limited effect on the density and stand structure of the dominant eucalypts (Murphy *et al.*, 2015, Fensham 2012), and eucalypt savanna woodlands are generally stable (Bowman *et al.* 1988, Fensham 1990, Bowman & Fensham 1991, Bowman & Panton 1996). However, *Melaleuca viridiflora* encroachment into some grasslands on Cape York Peninsula have been confirmed (Neldner *et al.* 1997, Crowley & Garnett 1998). Burrows *et al.* (2002) measured a mean net total carbon increase of 0.53 t C ha-1 y-1 across 57 Queensland woodland sites over 2-14 years, of which half is due to the increase in live above-ground biomass stocks. They reference woody thickening occurring in Africa, North and South America as well as in Australia.

Australian tropical savannas have been identified as an ecosystem under collapse, at least locally, by Bergstrom *et al.* (2021) because of the pressures of global changing temperatures and precipitation, and regional human pressures of habitat loss, invasive species (feral predators and weeds particularly gamba grass), livestock grazing and human-lit fire.

Aim of this study

The four sites in this study in tropical north Queensland have been monitored over a longer period (30 years) than the Northern Territory studies, and while not manipulated experiments, have experienced up to eight fires and varying magnitude of annual rainfall over the long study period. These ‘natural experiments’ are an important contributor to our understanding of the impact of fires on biodiversity (Williams *et al.* 2003b, Woinarski *et al.* 2004). The four sites with their altitude and rainfall gradient also straddle the boundary between the typical tropical savannas of the Einasleigh Uplands, and more mesic woodlands/open forest of the Wet Tropics bioregion. The aim of this study was to examine the dynamics of the woody layers of the vegetation in these monsoonal savannas of northern Queensland.

Methods

Study Sites

Four sites were located within a 20 km radius of Mareeba, north Queensland (Fig. 1) in four eucalypt communities across an altitudinal range from 380 to 840 m above sea level. This gradient was reflected by average annual rainfall ranging from 997 (site 1) to 1457 mm (site 4). The mean monthly and annual rainfall of all four sites was modelled using the SILO Data Drill system of the Queensland Department of Environment and Science (Jeffrey *et al.* 2001). The Data Drill produces synthetic climate data for any location by modelling and interpolation of point Bureau of Meteorology station records. The *Eucalyptus platyphylla, Eucalyptus leptophleba* open woodland (site 1) experiences a similar climate to Mareeba, which has a highly seasonal rainfall pattern of wet summers and very dry winters, typical of the tropical savannas of northern Australia. The *Eucalyptus reducta* open forest (site 4), because of its elevation and landscape position, experiences a higher annual rainfall and significant rainfall during the winter months. The *Corymbia clarksoniana* woodland (site 2) and *Eucalyptus reducta* open forest experience a climate typical of the western part of the Wet Tropics bioregion, whereas the *Eucalyptus platyphylla* open woodland and *Eucalyptus granitica* woodland (site 3) are in regional ecosystems typical of the Einasleigh Uplands bioregion (see Fig. 1). The site characteristics, together with the frequency of fires and grazing impacts being recorded, are summarised in Table 1, with regional ecosystem mapping information and statistics derived from Accad *et al.* (2019), Addicott & Newton (2012), and Queensland Herbarium (2021).

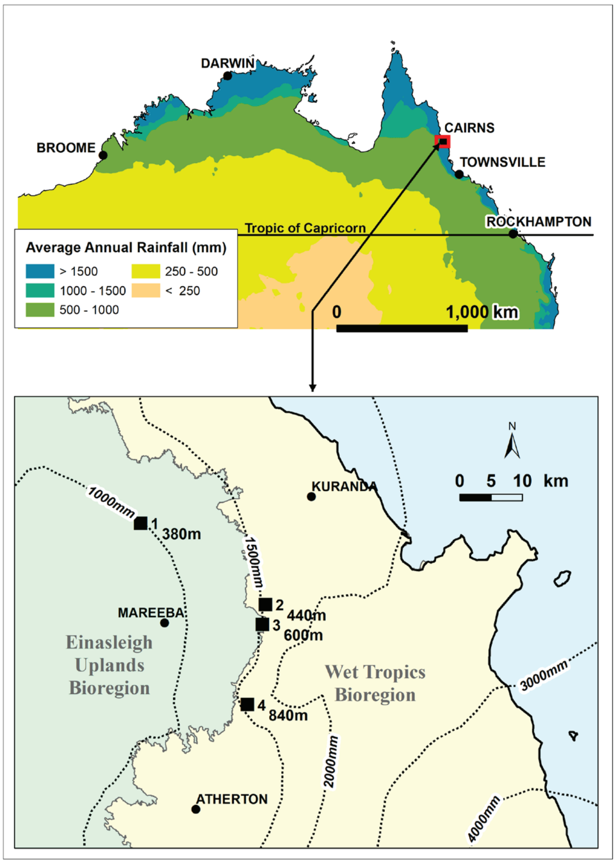

Figure 1. Map showing location for four monitoring sites, in relation to Australia's tropical savannas as defined by Fox *et al.* (2001).

Table 1. Monitoring site characteristics – location, fire history, vegetation and landscape.

Site No.	Tenure	Location of origin of site (Geographic Datum of Australia 1994)	Elevation (m above mean sea level)	Mean annual rainfall (mm)	No. of samplings when grazed†	No. of fires during sampling period	Regional Ecosystem, & remnant extent in 2019#	Dominant structure and canopy species at site, with height range of canopy and tree basal area (BA), and landscape position
1	Road reserve	-16.853674 145.388582	380	962	0	1	9.5.9b 15,880 ha	*Eucalyptus platyphylla* and *E. leptophleba* grassy open woodland (15-20m tall) (BA 5 m²/ha) on depositional plain
2	Grazing lease, Dinden State Forest	-16.970556 145.568054	440	1341	5	8	7.11.21a 12,178 ha	*Corymbia clarksoniana* woodland (14-20 m tall) (BA 12 m²/ha) with *Eucalyptus leptophleba*, *E. platyphylla* and *C. dallachiana* on lower slopes of metamorphic range
3	Davies Creek National Park	-16.999235 145.563478	600	1282	0	8	9.11.4a 27,111 ha	*Eucalyptus granitica* woodland (18-22 m tall) (BA 8 m²/ha) with *Corymbia citriodora, C. clarksoniana* and *Erythrophleum chlorostachys* on ridge crest of metamorphic range
4	Grazing lease, Danbulla State Forest	-17.114449 145.54194	840	1420	6	7	7.12.27a 16,027 ha	*Eucalyptus reducta* and *Corymbia intermedia* open forest (22-25 m tall) (BA 18 m²/ha) with *C. citriodora* and *E. granitica* on upper slope of steep granite range

†Sites 1, 2 and 3 were sampled on 12 occasions. Site 4 was sampled on 11 occasions.

Evidence of grazing included faeces of domestic stock, hoof prints and eaten plant parts

#Regional ecosystems are described in Queensland Herbarium (2021) and their 2019 remnant extent documented in Accad *et al.* 2021.

Field sampling

The vegetation survey site sampling methods adopted by the Queensland Herbarium have been summarised and fully discussed by Neldner *et al.* (2020). In summary, a single 50 m transect was established at each site and permanently marked at both ends with steel pickets. All individual woody plants occurring two metres on either side of the centre line were located as grid coordinates, identified, and the number of stems and maximum height recorded at each sampling. The numbers and species of woody plants recorded is summarised in Table 2. The woody plants were assigned a growth form following the definitions in Hnatiuk *et al.* (2009); Tree - a woody plant more than 2 m tall usually with a single stem; and Shrub - a woody plant, multi-stemmed at the base (or within 20cm from ground level), if single-stemmed then less than 1.5m tall. A Low Tree ranged in height from 1.5 to 5 metres. The shrubs were classified into the species that had the potential to grow into the canopy (i.e. juvenile trees) and those that always remained as shrubs. The woody forb *Stylosanthes scabra* is classified as a non-native shrub in this study. The data on the survivorship of individual trees and shrubs are summarised in Table 4 and 5 for sites 2 and 3, which contained the largest number of shrubs or juvenile canopy trees.

A strength of this study is that the same botanist (Neldner) conducted the sampling and species identification at each measurement to ensure consistency over the 30 years of sampling.

Table 2. Numbers of individuals of native tree and shrub species recorded at the four sites (200 m² plot) over the 30-year period

Site	Mean stem density/ ha. of canopy trees (T1) (max.)	Mean and range of stem density/ ha in T1 the same RE	Mean stem density of low trees (T2) (>2m) (max.)	Mean and range of stem density/ ha in T2 the same RE	Mean no. of shrubs of canopy species (max)	Mean no. of native shrubs of non-canopy species (max)	Mean and range of stem density/ ha in S1 the same RE	Species of Canopy tree	Native species of shrub and low tree (apart from juveniles of canopy trees)
1	100 (250)	182 (140 -260)	15 (50)	360 (140-480)	75 (300)	1920 (3950)	502 (100 -1060)	*Eucalyptus leptophleba, E. platyphylla*	*Grewia savannicola, Dolichandrone heterophylla*
2	275 (350)	285 (180-425)	590 (800)	286 (180-425)	1730 (2050)	1875 (5200)	4018 (1700-6250)	*Corymbia clarksoniana, C. dallachiana, Eucalyptus leptophleba, E. granitica, E. platyphylla*	*Jacksonia thesioides, Lamprolobium fruticosum, Melaleuca viridiflora, Petalostigma banksii, P. pubescens*
3	155 (200)	210 (160 -260)	350 (650)	80	1170 (1700)	1120 (1550)	160 (120-200)	*Corymbia citriodora, C. clarksoniana, C. dallachiana, Erythrophleum chlorostachys, Eucalyptus granitica*	*Melaleuca viridiflora, Petalostigma banksii, Bursaria incana, Grevillea glauca,*
4	155 (200)	301 (100-800)	225 (400)	416 (125-960)	240 (500)	170 (500)	1836 (40 -4000)	*Corymbia intermedia, Eucalyptus granitica, E. reducta*	*Allocasuarina torulosa, Persoonia falcata*

This study sampled the woody layer on 12 occasions, once in February (2016), four times in April (2007, 2008, 2009, 2010), three times in May (2001, 2004, 2021), once in June (2020) and three times in November (1991,1992, 1993), over the 30-year period (1991 -2021). The *Eucalyptus reducta* site was not sampled in 2018 as it was inaccessible because of a road blockage. The tree canopy cover was measured on 15 occasions in May. Photographs of the site were taken at each sampling, and voucher specimens collected, identified, and lodged at the Queensland Herbarium. Plant nomenclature follows Brown and Bostock (2020). The families and genera represented in this study are typical of the flora of the Australian tropical savannas (Clarkson & Kenneally 1988).

Data collation

While all four sites were generally measured at the same sampling time, in 2015 only sites 1, 2 and 4 were measured and site 3 was measured in 2016. We have combined these two years into one combined measure of 2015-16 and averaged the rainfall for those two years. As the *E. reducta* site was not measured in 2018 we have interpolated the data between 2015 and 2020.

To understand changes in the vegetation structure, species were divided into those which could occur in the canopy layer (canopy-species, e.g. *Eucalyptus* spp., *Corymbia* spp. and *Erythrophleum chlorostachys*), and those, which would never grow into the canopy layer (non-canopy-species, e.g. *Grewia savannicola, Acacia* spp., etc). Each site in each year of measuring was treated as one record. There was a total of 48 records and 31 species in the dataset.

The number and timing of fires at each site was compiled from field observations at the time of sampling (quarterly for the first three years (Neldner *et al.* 2004, Neldner 2021), and a further 15 occasions in May (Neldner & Butler 2021) and a further two in December, fire mapping from the Digital Earth Australia Hotspots (2002 to present) (Australian Government 2022), fire scar mapping by DES (1995-present) (Queensland government 2021) and for all sites except the *Eucalyptus platyphylla, Eucalyptus leptophleba* woodland site the Queensland Parks and Wildlife Service fire mapping (R. Miller, pers comm). The months-since-fire is recorded from November 1991, when the first sampling was conducted. The months-since-fire prior to the first sampling in November 1991 was calculated differently for each site and based on the average period between fires during the sampling period where no other information was available. For the *Eucalyptus granitica* woodland there was a fire scar from a fire three months prior to sampling (September 1991). For the *Eucalyptus platyphylla, Eucalyptus leptophleba* woodland site there was only one fire across the 30-year period and so half of the average fire interval for the site was used (180 months). For the *Corymbia clarksoniana* woodland and the *Eucalyptus reducta* woodland sites the average fire interval for each site was used (45 months and 51 months respectively). This recorded information was compared with the fire management guidelines for the community at each site (Queensland Herbarium (2021) to understand how closely the recorded fire history matched the recommended guidelines. The dry season was divided into three time-frames; the early dry season (April – June), the mid dry season (July – August) and late dry season and storm burns (September – November). Where the intensity of the fire was not recorded it was assumed that early dry season burns were low intensity, mid dry season burns were moderate intensity and late dry season were high intensity fires.

Data analysis

As each site was in a different regional ecosystem (plant community) and spanned a 30-year sampling period, the variability in the structure of the vegetation data was investigated. Outliers in the dataset across sites and years were assessed using a range of diversity indices and box and whisker plots. The indices used were species diversity (Shannon's diversity index), species richness (Margalef's index, which corrects for the expectation that a larger number of individuals in a survey is likely to increase the number of species), evenness (Pielou's index) and total number of individuals. Changes in abundance of native species were investigated at the individual site level.

To understand changes over time, the data was divided into shrub, low tree and canopy layers and changes investigated in each layer. The magnitude of the number of individuals of native species in each layer differed; the shrub layer dominated the dataset with an average of 65 canopy and 101 non-canopy individuals recorded at each sampling, while the canopy layer had an average of 14 and the low tree layer had an average of 24 individuals recorded (Table 2).

For the vegetation structure of a community to be maintained the canopy species juveniles must live long enough to grow into the canopy layer. To measure this, the change in the proportion of canopy-species individuals making up the shrub layer and the low tree layer over the 30-year period was tested using Fisher's exact test and a 2x2 contingency table (GraphPad online software (Analyze a 2x2 contingency table (graphpad.com) accessed 11/02/21).

Results

Data structure

As expected with sites in different plant communities, there were distinct differences in species composition between sites. This was reflected in the data structure; between sites there was a substantial difference in all diversity measures however this was not significant and despite the low numbers of individuals in the *Eucalyptus platyphylla, Eucalyptus leptophleba* open woodland in 1991 it was not an outlier. There was no significant variation between years in the total number of individuals measured or the species richness, evenness and species diversity.

Rainfall

The average annual rainfall (1991-2020) for the nearest towns of Mareeba and Atherton was slightly lower (96 and 97% respectively) and the range of annual totals (63 and 68% less) during the study period as compared with the period 1900-1990 (SILO data). While the actual amount of rainfall received varied during the sampling period with below average rainfall years 1992-93, 1995, 2002-2003 and 2015-16 (<60% of mean annual rainfall), and above average rainfall in 1999-2001, 2004, 2008, 2011-12 and 2018 (>150% of mean annual rainfall) the seasonal distribution of rainfall was typical of the long-term rainfall pattern and there was a gradual drying trend over the last 60 years (Fig. 2)

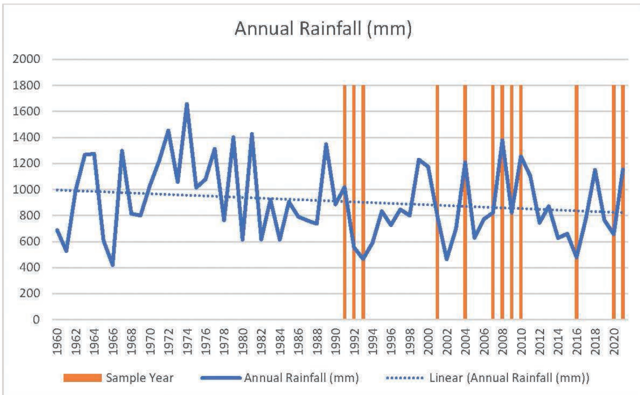

Figure 2. Mean annual rainfall for Mareeba post office (1960-2022) derived from Bureau of Meteorology website and sampling dates.

Fire history

There were 17 years in which fire occurred in at least one site over the 30-year period (Table 3). The maximum number of sites burnt in any one year was three (2002 and 2005), with the maximum number of times any one site burnt being eight. The *Corymbia clarksoniana* and the *Eucalyptus granitica* woodland sites were burnt eight times and the *Eucalyptus reducta* open forest seven times. In contrast, the *Eucalyptus* *platyphylla, Eucalyptus leptophleba* open woodland was burnt once. (Table 3). The fire management guidelines for all four communities recommend a fire interval of 2 – 5 years; low, with occasional moderate, intensity burns; and occurring in the early dry season with occasional burns in the storm season. The only fire in the *Eucalyptus platyphylla, Eucalyptus leptophleba* woodland occurred in the late dry season (equating to a high intensity fire) and the fire-interval was a minimum of 15 years. At the other three sites the fire intervals ranged from 1 – 11.8 years. The sites with the greatest number of fires, the *Corymbia clarksoniana* and the *Eucalyptus granitica* woodlands, averaged fire intervals of 3.7 years (range 1.2 – 5.1*)* and 3.3 years (range 2 – 10.75) respectively, both within the recommended guidelines. In the *Eucalyptus reducta* woodland site the average fire interval was 5.9 (range 1 – 11.8) years, a little over the recommended interval. The majority were moderate to high intensity, occurring in the mid to late dry season. Most of the fires at the sites occurred in the mid dry season (58% moderate intensity), the next most in the late dry season (29% high intensity) and only 13% occurred in the early dry season (low intensity). At the time of samplings, the impacts of the fires were observed to burn through the whole of the study sites.

Table 3. Recorded fire history at individual sites.

The number and timing of fires at each site was compiled from field observations at the time of sampling, fire mapping from the Australian Government Sentinel Hotspots program (2002 to present), fire scar mapping by DES (1995- present) and, for all sites except the *Eucallylptus platyphylla, E. leptophleba* woodland site, the Queensland Parks and Wildlife Service fire mapping (R. Miller, pers comm).

Year	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**No. sites burnt**	
	E. platyphylla, E. leptophleba woodland	*C. clarksoniana* woodland	*E. granitica* woodland	*E. reducta, C. intermedia* open forest		
1991*			Sep-91		1	**November = first sample*
1992				Aug-92	1	
1993		Aug-93			1	
1994					0	
1995					0	
1996					0	
1997					0	
1998					0	
1999		Aug-99			1	
2000					0	
2001				Aug-01	1	
2002		Oct-02	Aug-02	Aug-02	3	
2003					0	
2004					0	
2005		Sep-05	Aug-05	Aug-05	3	
2006					0	
2007	Sep-07				1	
2008			Aug-08		1	
2009		Jul-09			1	
2010			Aug-10		1	
2011					0	
2012					0	
2013			Jul-13		1	
2014		Aug-14		Oct-14	1	
2015					0	
2016		Oct-16	Jul-16		2	
2017				May-17	1	
2018					0	
2019			May-19	Nov-19	2	
2020		May-20			1	
2021					0	**May = last sample*
Total no. fires / site	1	8	8	7		

Vegetation

Site 1 *Eucalyptus platyphylla, Eucalyptus leptophleba* open woodland

Shrub layer

There was a large increase in the number of shrubs over the sampling period (from two in 1991, to 15 in 1992 and finally 87 in 2021). The increase was due to an increase in non-canopy species shrubs (Fig 3). There was only one fire at this site in 30 years.

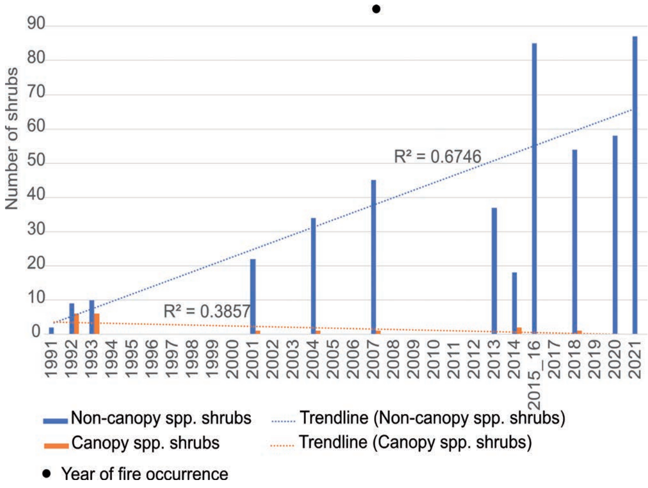

Figure 3. The number of native shrubs and occurrence of fire at the *Eucalyptus platyphylla, E. leptophleba* open woodland (site 1) over the sample period. The mean annual rainfall is 932 mm.

The number of individuals of canopy-species in the shrub layer varied over time, but overall decreased from six in 1992 and 1993 to zero in 2021. The change in proportion of canopy-species to non-canopy species shrubs between 1992 (the first year canopy-species were recorded in the shrub layer) and 2021 was extremely significant ($p < 0.0001$).

The *Eucalyptus platyphylla, Eucalyptus leptophleba* open woodland had a low density of shrubs from 1991-93 that included *Eucalyptus platyphylla,* the dominant tree. The only fire at the site occurred in April 2007, and all samplings after this recorded relatively high densities of the multi-stemmed subshrub *Grewia savannicola.* The subcanopy low tree *Dolichandrone heterophylla* was consistently present as a shrub, while the *Eucalyptus platyphylla* shrubs were absent in the later years. The non-native pasture legume *Stylosanthes scabra* was first recorded as an individual at the site in 2001. It was recorded for the first time in a nearby grazed site in 1998 (Neldner & Butler 2021). After 2001 *Stylosanthes scabra* increased rapidly in density in later years (250 individuals per hectare in 2007, 650 in 2013, 1700 in 2014 to 6400 per ha in 2021).

Low tree layer

There was one individual recorded in the low tree layer in the *Eucalyptus platyphylla* woodland in 1991, 1992 and 1993. This individual had disappeared from the low tree layer but not recruited to the canopy layer at the next sampling (2001) and no individuals were recorded in the low tree layer thereafter.

Canopy layer

The number of canopy trees fell from five in 1991 to one in 2021. The loss of two *Eucalyptus leptophleba* trees (14.5 and 15.5 metres tall) and two *Eucalyptus platyphylla* trees (12.5 and 13m tall) occurred between 1993 and 2001, with the number of canopy species remaining at one after 2001 (Fig 4). The decline in numbers of canopy trees is evident in comparison photographs taken at the origin of the site (Fig. 5).

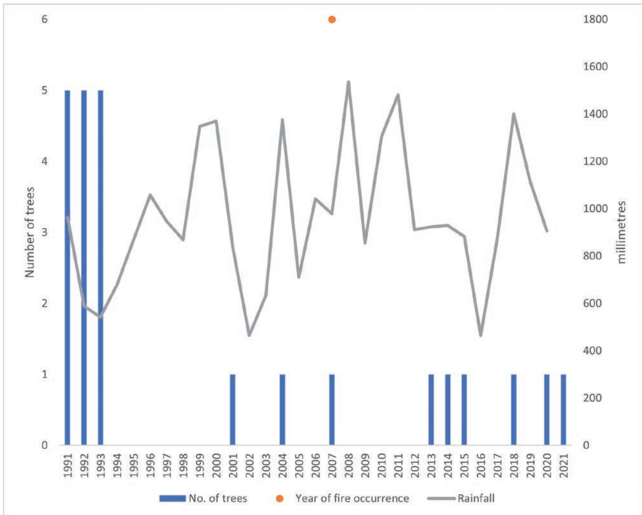

Figure 4. The number of canopy trees, occurrence of fire and annual rainfall (mm) at the *Eucalyptus platyphylla, E. leptophleba* open woodland (site 1) over the sample period. The mean annual rainfall is 932 mm.

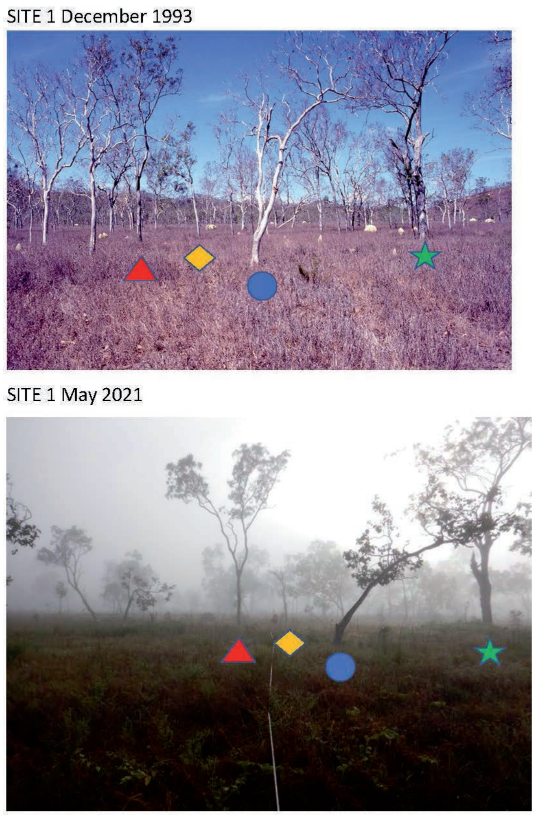

Figure 5. Photographs taken at the origin of *Eucalyptus platyphylla, E. leptophleba* open woodland (site 1) in December 1993 and May 2021. Symbols denote individual trees.

Site 2 *Corymbia clarksoniana woodland*

Shrub layer

The number of shrubs in the site varied across the sampling period, with a general increase between 1991 (*n = 33*) and 2021 (*n = 86*). The increase occurred in both canopy-species individuals and non-canopy species individual. There was a peak in 2018, the year of highest rainfall (2263 mm) (Fig 6). The proportion of canopy-species individuals in the shrub layer fluctuated between a low of 32% (in 2018) and a high of 60% in 2014.

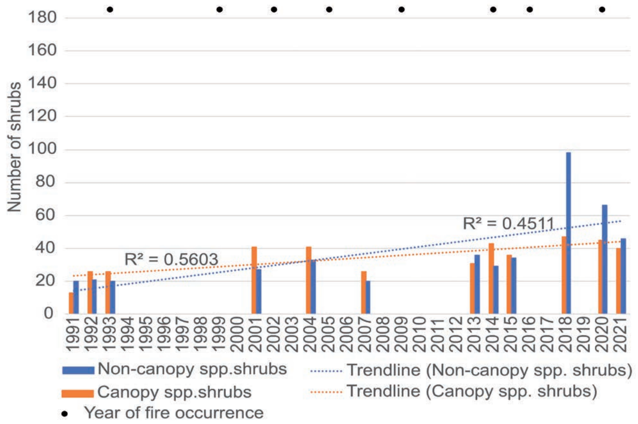

Figure 6. The number of native shrubs and occurrence of fire at *Corymbia clarksoniana* woodland (site 2) over the sample period.

There were consistent shrub densities of the canopy species *Corymbia clarksoniana* and *Eucalyptus platyphylla*, and low tree species of *Melaleuca viridiflora, Petalostigma banksii* and *Planchonia careya.* The facultative seeders *Acacia leptostachya* and *Jacksonia thesioides* were consistently present at the site after the first recorded fire in August 2000, and another facultative seeder *Lamprolobium fruticosum* from the 2007 sampling. These facultative seeding shrubs were all present in the nearby area prior to be recorded in the site.

Low tree layer

The number of low trees varied over the 30-year period, with a low of seven in 2015 and a high of 16 in 2013. The number of canopy-species in the low tree layer however decreased consistently from six in 1991 to one in 2021 (Fig 7.). The decrease in the proportion of canopy-species was significant (*p = 0.02*) falling from 60% in 1992 to 9% in 2021.

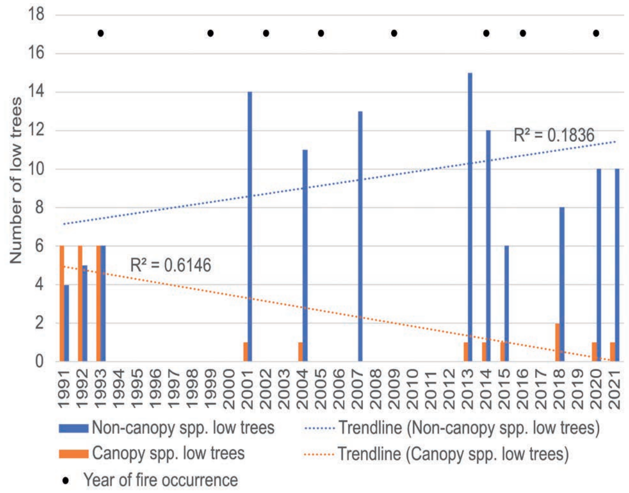

Figure 7. The number of low trees and occurrence of fire at *Corymbia clarksoniana* woodland (site 2) over the sampling period

Canopy layer

The number of trees in the canopy layer decreased from seven in 1991 to four in 2021, but is not obvious in the comparison photographs taken at origin of the site (Fig. 8), as the tree deaths occurred at the far end of the plot.

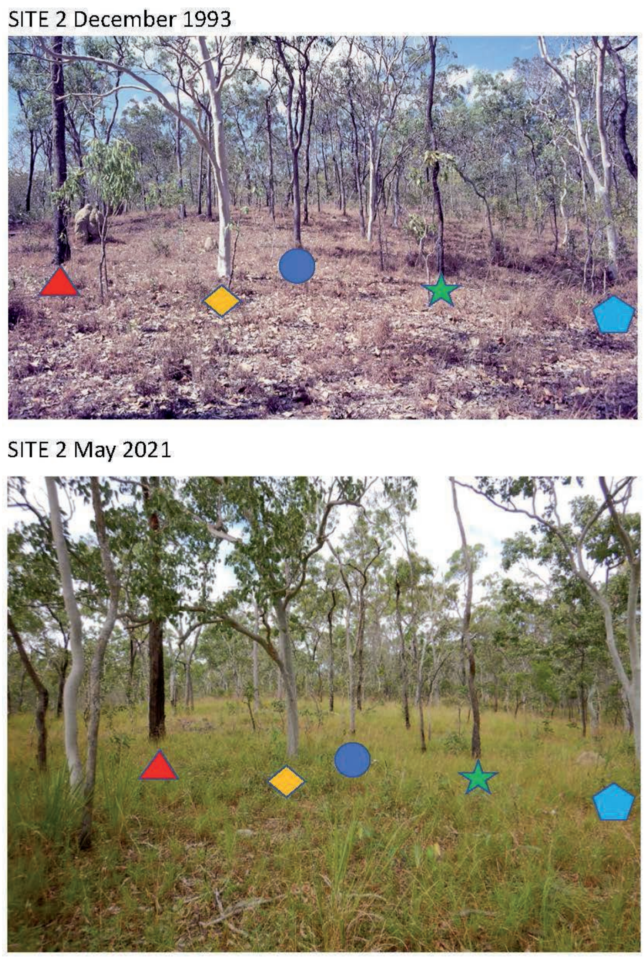

Figure 8. Photographs taken at the origin of *Corymbia clarksoniana* woodland (site 2) in December 1993 and May 2021. Symbols denote individual trees.

Site 3 *Eucalyptus granitica* woodland

Shrub layer

The number of shrubs varied between sampling times from a minimum in 1991 (*n = 27*) to 24 in 2021 with a peak in 2001 (*n = 65*) (Fig 9). The change in the proportion of canopy-species to non-canopy species in the shrub layer did not show any distinct pattern (Fig. 9).

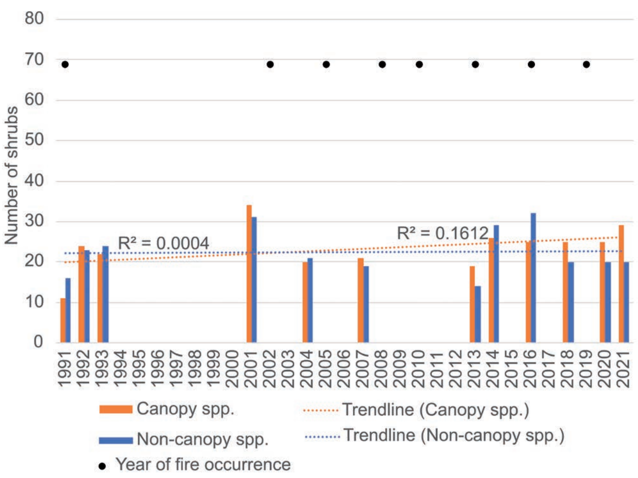

Figure 9. The number of native shrubs and occurrence of fire at *Eucalyptus granitica* woodland (site 3) over the sampling period.

The *Eucalyptus granitica* woodland was burnt seven times and recorded similar consistent low shrub densities of canopy-species (*Corymbia clarksoniana*, *Eucalyptus granitica* and *Erythrophleum chlorostachys*), and the low tree species (*Bursaria incana*, *Melaleuca viridiflora* and *Petalostigma banksii*) during the sampling period. Despite frequent fires, the facultative seeders of *Acacia leptostachya*, *Jacksonia thesioides*, and *Lamprolobium fruticosum* did not occur on the site, although they did occur on the abandoned road nearby. In 2014, *Stylosanthes scabra* was recorded for the first time at a density of 420 individuals per hectare, increasing rapidly in density in later years (1100 in 2016, 980 in 2018 to 2740 per ha in 2021).

Low tree layer

There was an overall increase in the total number of low trees which varied over the 30-year period. They increased between 1991 and 2016 and then decreased by 53% in 2018 and remained at this number through to 2021 (Fig 10). The proportion of canopy-species low trees increased from 0 in the first three years to 25% in 2001. This is most likely explained by some of the canopy species shrubs growing into low trees (>1.5 m tall) in the 10 year period without a fire. It thereafter fluctuated between 17% and 46% throughout the rest of the sampling period, although none of the changes in proportion were statistically significant (Fig. 10).

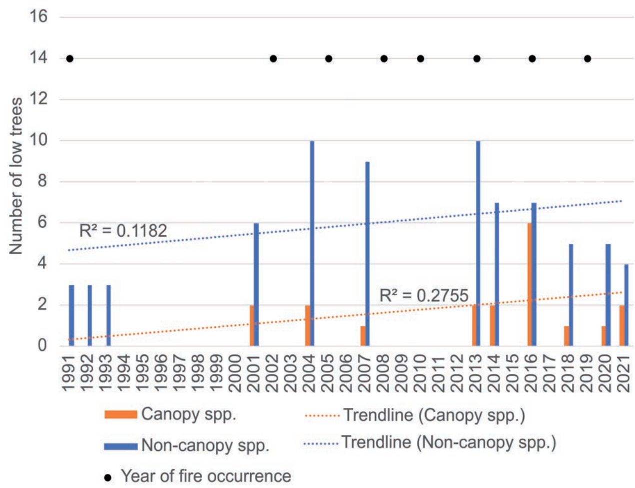

Figure 10. The number of low trees and occurrence of fire at *Eucalyptus granitica* woodland (site 3) over the sampling period.

Canopy layer

There was no change in the overall numbers of canopy trees over the sampling period. The large *Eucalyptus granitica* tree that is absent in the 2021 comparison photographs taken at origin of the site (Fig. 11) was already dead at the initial sampling in November 1991.

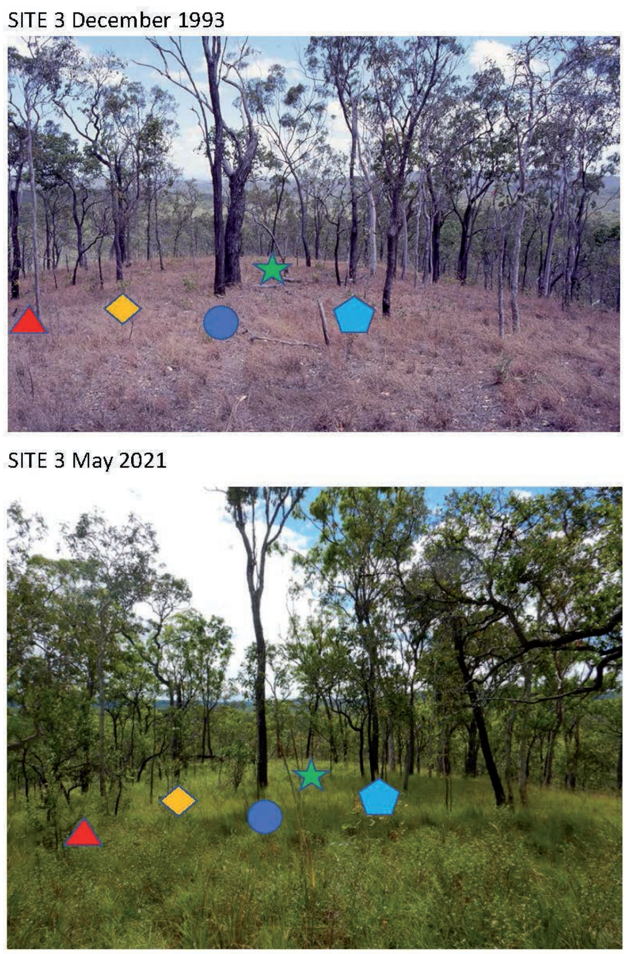

Figure 11. Photographs taken at the origin of *Eucalyptus granitica* woodland (site 3) in December 1993 and May 2021. Symbols denote individual trees.

Site 4. Eucalyptus reducta woodland

Shrub layer

While always low in this site, the number of shrubs varied over the sampling period (Fig. 12). The proportion of canopy-species to non-canopy species individuals at this site was always high but dropped overall from 100% in 1991 to 69% in 2021. Individual shrubs of the canopy-species *Eucalyptus reducta* and *Corymbia intermedia* were consistently present, in the early samplings at higher densities than post the fires in October 2001 and December 2002.

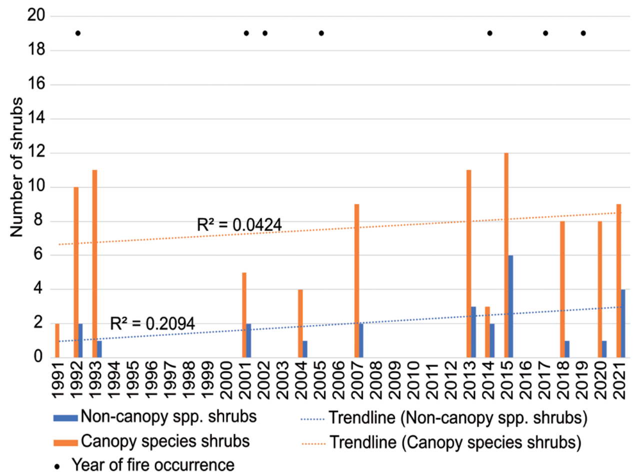

Figure 12. The number of native shrubs and occurrence of fire at *Eucalyptus reducta* open forest (site 4) over the sampling period.

Low tree layer

All the individuals in the low tree layer were canopy-species. The number of low trees declined by 87.5% between 1991 and 2021, with the largest loss of low trees through death between 2013 – 2018 (Fig. 13). The density of low trees of *Allocasuarina torulosa* were consistently lower after the fires of October 2001 and December 2002.

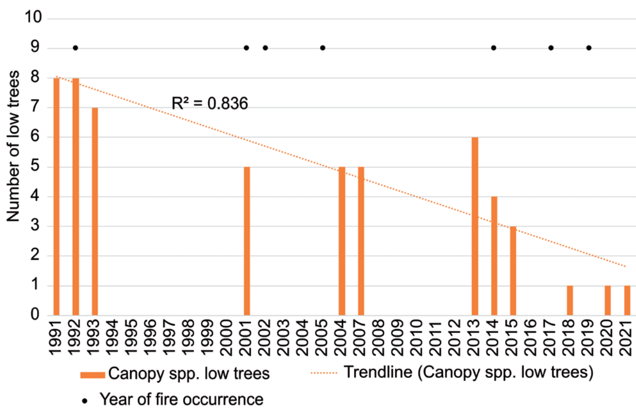

Figure 13. The number of low trees and occurrence of fire at *Eucalyptus reducta* open forest (site 4) over the sampling period.

Canopy layer

The number of trees in the canopy layer declined from four to three over the 30-years sample period. A large *Eucalyptus reducta* tree was killed by fire in October 1994 (Fig. 18). The 2021 photograph taken at origin of the site (Fig. 14) shows a sparser canopy and *Allocasuarina torulosa* subcanopy tree layer than that taken in December 1993.

Figure 14. Photographs taken at the origin of *Eucalyptus reducta* open forest (site 4) in December 1993 and May 2021. Symbols denote individual trees.

Persistence of individual shrubs and low trees

Most native shrubs of both canopy and non-canopy species only persisted for short periods. The smallest stems are generally most susceptible to top kill (all the above-ground tissue killed) by fire, but even large trees can be susceptible if they are hollow from termite damage and fires can burn from the inside out (Williams *et al.* 1999). In the *Corymbia clarksoniana* woodland, the exceptions were two shrubs of the canopy species *Corymbia clarksoniana*, and four of *Eucalyptus platyphylla*, and 11 of the non-canopy species *Melaleuca viridiflora*, and one of *Planchonia careya* (see Figure 15). These were still alive after 7-21 years having survived five fires at the site. In most cases these individuals remained as shrubs less than 2 m tall, except for three *Melaleuca viridiflora* that were still alive after 24 years. These had grown through to small trees 3-5 metres tall. There was an individual of the canopy-species *Eucalyptus platyphylla* shrub that germinated and established between 1994 and 2000 and was first recorded in 2001 as a single stemmed shrub 1.3 m tall. It was recorded another eight times between 2001 and 2018, ranging in height from 0.7 to 5 metres tall with between one and four stems, surviving five fires (November 2002, October 2005, June 2009, August 2014, July 2016). It was not recorded in 2020, presumably being killed in the May 2020 fire. (Fig 14)

Table 4. Age of death of individual shrubs by species at *Corymbia clarksoniana* woodland (site 2). The number of fires survived is in brackets.

Species	<1 year	1-2 years	3-6 year (1,2)	7-21 years (5)	22-30 years (6)
Acacia leptostachya	8	0	0	0	0
Corymbia clarksoniana	33	11	10	4	1
Eucalyptus granitica	3	0	0	0	0
Eucalyptus leptophleba	0	0	1	0	0
Eucalyptus platyphylla	2	1	2	1	0
Jacksonia thesioides	26	0	3	0	0
Lamprolobium fruticosum	9	0	0	0	0
Melaleuca viridiflora	9	7	2	0	3
Petalostigma banksii	2	1	2	1	0
Petalostigma pubescens	2	0	4	0	0
Planchonia careya	1	0	0	0	0

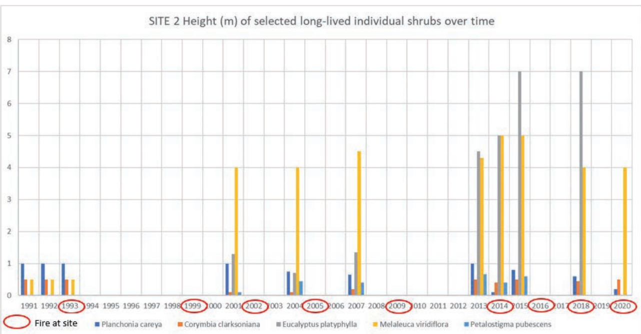

Figure 15. Height of selected long-lived individual native shrubs at *Corymbia clarksoniana* woodland (site 2)

Table 5. Age of death of individual shrubs by species at *Eucalyptus granitica* woodland (site 3). The number of fires survived is in brackets.

Species	<1 year	1-2 years	3-6 year (1,2)	7-21 years (5)	22-30 years (6)
Corymbia clarksoniana	14	0	1	0	0
Erythrophleum chlorostachys	8	2	1	1	0
Eucalyptus granitica	10	0	2	0	0
Grewia savannicola	3	0	0	2	0
Melaleuca viridiflora	13	7	3	1	1
Petalostigma banksii	8	3	0	1	1

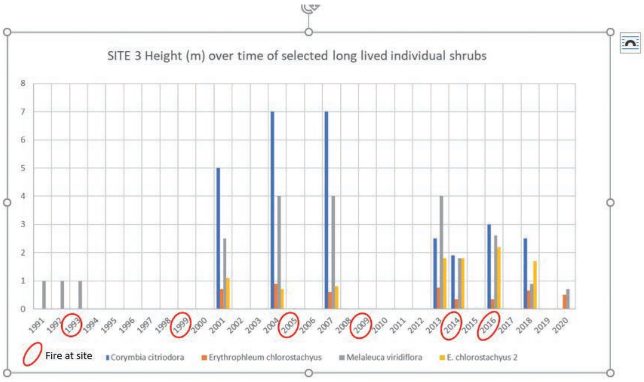

Figure 16. Height of selected long-lived individual native shrubs at *Eucalyptus granitica* woodland (site 3)

In the *Eucalyptus granitica* woodland (site 3), there was one shrub of *Corymbia clarksoniana*, one of *Corymbia citriodora*, nine shrubs of *Erythrophleum chlorostachys*, four of *Melaleuca viridiflora*, three of *Eucalyptus granitica*, seven of *Petalostigma banksii* and three of *Grewia savannicola* that have survived five fires at the site and were still alive after 7-24.5 years (Table 5). In most cases they remained as shrubs less than 2 m tall, apart from the *Corymbia citriodora* which was first recorded in May 2001 as a 5 metre low tree (appeared since the November 1993 sampling), and reached a height of seven metres in 2004, before being burnt and top killed in a fire in September 2005, and resprouting as a shrub, being recorded as two stems 1.85 m tall in April 2007, survived additional fires in September 2008 and August 2014, and persisted as a low tree 2-3 metres tall in February 2016 and July 2018. It appears to be killed in 2019 fire, as it was not recorded in the June 2020 sampling (Fig.16).

Non-native woody species

The woody shrubs of *Stylosanthes* spp. mostly *Stylosanthes scabra* had been recorded in the ground layer in 2000 in the *Eucalyptus granitica* woodland, and 2001 in the *Eucalyptus platyphylla, Eucalyptus leptophleba* and *Corymbia clarksoniana* woodlands (Neldner and Butler 2021). While not persisting in the *Corymbia clarksoniana* woodland, there has been an exponential increase in the density of *Stylosanthes* spp. in the other two sites. (Fig. 17).

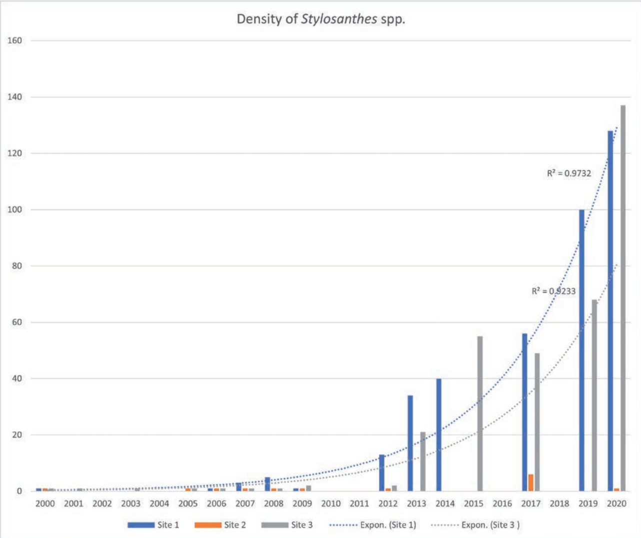

Figure 17. Stem density and trendline of *Stylosanthes* species since first detection in 2000 for three sites.

Discussion

This study, conducted over thirty years, represents the only long-term vegetation monitoring study in the north Queensland tropical savannas. Across the four sites, representing different plant communities of the mesic savanna in northern Queensland, and over three decades, there was a general increase in the density of native shrubs and decrease in the density of the low tree layer and canopy layer. There were no individuals of canopy-species plants which grew into the canopy. In three out of four sites there was a reduction of the canopy layer and canopy-species individuals in the low tree layer, to densities below the average for their respective regional ecosystem. The 1992-1994 period was very dry and may have contributed to the loss of some trees at site 1 and 2, but shorter dry periods also occurred during the monitoring period with no apparent canopy tree loss. The average rainfall for Mareeba Post Office from SILO since 1889 (132 years) was 932 mm, and there has been a general downward trend since 1889.

Cairns experienced some impact from six tropical cyclones during the sampling period (Justin 1997, Rona 1999, Steve 2000, Abigail 2001, Larry 2006 and Yasi 2011). The most powerful Larry category 4 and Yasi category 5, produced destructive winds on the Atherton Tableland, when they crossed the coast south of Innisfail. Cyclones Abigail, Steve, Rona and Justin were category 2 cyclones that headed west from just north of Cairns and weakened rapidly after crossing on to land. There was no evidence of widespread damage in news reports or observed at the sampling sites, so it is unlikely that this was a cause of tree loss at the study sites.

When the fire regime at each site was examined and compared to the recommended fire management guidelines, the interval between fires was within the guidelines, but the season (and consequent intensity) of fires was not. Fires were predominantly more intense than recommended and carried out in the mid to late dry season. Although the interval is within guidelines, the effect of fires occurring when there is a moisture deficit in the trees is overwhelming any effect of the correct fire interval. These results appear to highlight the importance of reducing the intensity of fires occurring in these communities. Climate change predictions for the tropics include longer and warmer dry seasons (IPCC 2014) leading to smaller windows for low intensity burns. Without careful management the trend to lose canopy trees may result in less dense woodlands and forests, significantly changing the structure of savanna woodlands.

Loss of canopy trees

In three of the four sites there was a loss of individuals in the canopy. The *Eucalyptus granitica* site maintained the overall number of canopy trees. This site had a dead *Eucalyptus granitica* canopy tree at the initial sampling in 1991 and it remained standing until 2004 but was no longer present as coarse woody debris at 2006 (Fig.18). No canopy-species individuals progressed through into the canopy. Species that died during the time of observations were *Eucalyptus platyphylla* and *Eucalyptus leptophleba* (site 1), *Eucalyptus leptophleba* and *Corymbia clarksoniana* (site 2), *Eucalyptus granitica* (site 3), and *Eucalyptus reducta* and *Allocasuarina torulosa* in site 4. Most tree deaths followed the pattern of a progressive decrease in canopy cover, followed by some successive years of weak epicormic shoots before the eventual death (Fig. 18). The soil was checked for any evidence of *Phytophthora* spp. by a plant pathologist, but no trace was detected. In December 2002 many *Eucalyptus reducta* trees lost most of their canopy in the *Eucalyptus reducta* open forest in the drought conditions (canopy cover only 13.5 %), and gradually recovered partial canopy in subsequent years through resprouting on the trunk. These observations are consistent with the conclusions of Fensham *et al.* (2005) and Murphy *et al.* (2015) that it is water availability that determines eucalypt biomass. There was no evidence of canopy loss by herbivory from insects or fungi.

A *Eucalyptus reducta* canopy tree died because the lower trunk was burnt in the October 2014 fire and it fell to the ground (Fig. 18). Site 1 which only experienced one fire over the 30-year period (another scenario for increased tree cover in Lehmann *et al*. 2009b) showed a decreased cover over time with the death and non-replacement of canopy eucalypts. In mesic savannas, the ground layer has the potential to compete with trees of all sizes for nutrients and water as shown in African, Australian and North American savannas (Menaut *et al.* 1990, Prior *et al.* 2006, Archer 1995). The amount and type of ground layer may impact on the degree of competition with the juvenile trees. Werner *et al.* (2013) contrasts the competition for nutrients between an annual sorghum ground layer and a perennial grass layer and illustrate that this also interacts with the fire behaviour with different ground layers. Fensham *et al.* (2005) found in a study of central Queensland savanna woodlands over a 50-year period that relative rainfall was positively related to rates of change in both the overstorey and the understorey woody vegetation, whereas the impacts of fire and grazing were not significant. They argue that periodic drought deaths of canopy trees maintain the open structure of north-eastern Queensland savanna, rather than bottlenecks in recruitment or sapling escape. The 2019-20 catastrophic fires in southern Queensland and Australia have been linked to severe moisture deficits and record-breaking temperature extremes which are likely linked to climate change, and it is expected this downward trend in tree cover will continue. In this study, the long-term drying trend in the rainfall with the inconsistent wet season has probably contributed to the death of many canopy trees through moisture stress particularly at sites 1 and 2, however the frequent fires are preventing canopy recruitment and directly caused the loss of a canopy tree at site 4.

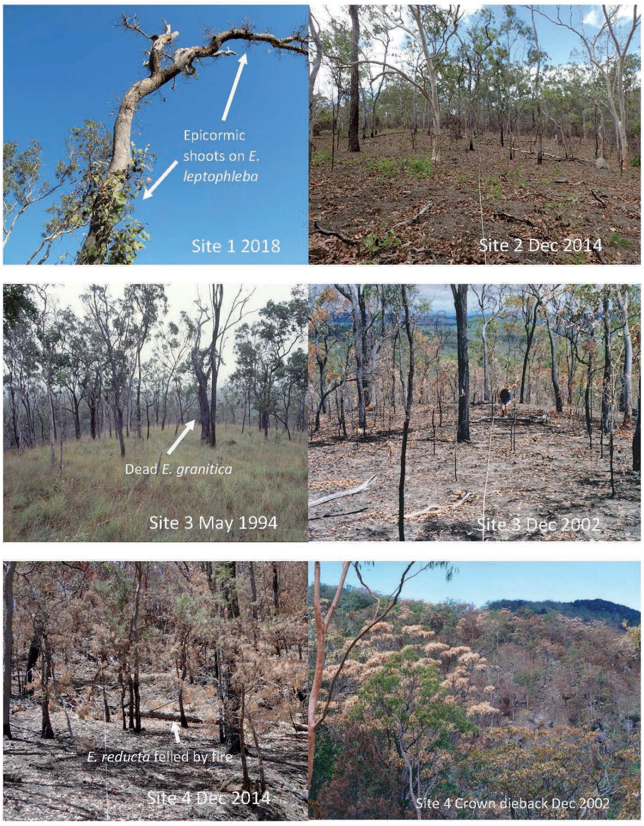

Figure 18. Progressive dieback of canopy of *Eucalyptus leptophleba* at site 1; resprouting shrubs after fire of *Corymbia clarksoniana, Eucalyptus leptophleba, Eucalyptus platyphylla* and *Corymbia dallachiana* at site 2; dead *Eucalyptus granitica* canopy tree present in 1994 but removed by fire in 2002 at site 3; living *Eucalyptus reducta* canopy tree felled by hot fire in October 1994 in site 4, and drought induced crown dieback in *Eucalyptus reducta, Corymbia intermedia* open forest with *Corymbia citriodora* and *Eucalyptus granitica* site 4 in December 2002.

The effect of yearly rainfall variation on the woody layers

The sites were deliberately selected to cover a gradient in the average annual rainfall (997 to 1457mm) and seasonality experienced at each site (50% (Site 4) to 58% (Site 1) of annual rainfall experienced in summer months). The 30 years of sampling (1991-2021) were slightly drier for sites 1 and 4, but slightly wetter for sites 2 and 3 compared to the long-term average rainfall for the area (Jeffrey *et al.* 2001). There were seven years with rainfall less than 60% of the long-term mean which produced moisture stress with this being manifest in widespread canopy leaf drop in the wettest site (4) in December 2002 (Fig. 18). Canopy leaf drop caused by moisture stress is not a frequent event in the predominantly evergreen eucalypt dominated tropical savannas in Queensland, however, did occur in substantial areas south of Cape Melville in July 2013 (Neldner & Addicott, pers comm). There were eight years with rainfall greater than 150 % of the mean at the study sites. There was a drying trend in the long-term rainfall pattern. However, there appeared a general increase in non-canopy shrub numbers over the 30-year period. In seasonally wet *Melaleuca viridiflora* woodlands on Cape York Peninsula, wetter than average years in the absence of fire produced elevated levels of seedling germination and survival, suckering and plant growth (Crowley *et al.* 2009). The fate of these seedlings/ shrubs was dependent on the occurrence and timing of burning, and the competition of the grass layer. As *Melaleuca viridiflora* leaves are unpalatable to cattle, any grazing present may favour their growth by reducing grass competition (Crowley *et al.* 2009).

Survivorship of shrub recruits

In the Australian mesic savannas such as in this study (997-1457 mm annual rainfall) and at Kapalga (1480 mm), there were an abundance of the juvenile tree size class (<2 m tall) here included in the shrub layer (Fensham & Bowman 1992, Wilson & Bowman 1994; Lehmann *et al.* 2009b). Local tree populations are characterised by very few saplings but several suppressed juvenile trees <2m tall of indeterminate age that have survived as multi-stemmed shrubs or lignotubers or resprouting from roots This situation of large juvenile tree banks, transition bottle necks and bimodal size structures has been reported for the savannas of north America e.g., Scholes & Archer 1997, Asia e.g., Baker & Bunyavejchewin 2006), Africa e.g., Bond & Midgley 2001) and Australia (Lehmann *et al.* 2009a, Werner & Prior 2013). The process of recruitment involves both facultative seeders and resprouters (Lacey & Whelan 1976). Seedling recruitment is infrequent and patchy in eucalypt savannas (Setterfield 2002; Williams 2009). For the canopy species which are all eucalypts (and *Erythrophleum chlorostachys* in site 3), the recruitment is based on the infrequent germination of seed, which may grow and persist as shrubs (resprouting after fires) for a considerable period, before some may grow into canopy trees.

This typical savanna structure is reflected in sites 2, 3 and 4 (Table 2), and the persistence and growth of individual plants has been tracked over 30 years. Once established, shrubs may develop lignotubers and are able re-sprout from these or underground roots after being burned in fires. Lawes *et al.* (2022) classified all the woody species at these sites to be epicormic resprouters, apart from *Grewia* spp. which were root resprouters, *Grevillea glauca* and *Bursaria incana* which were basal resprouters, and *Acacia leptostachya* and *Jacksonia* species which were killed by fire. *Lamprolobium fruticosum* and *Eucalyptus leptophleba* were not included in the classificationn by Lawes *et al.* (2022). The 'fire trap' hypothesis is that recruits need to rapidly grow to escape the fire recruitment bottleneck if they are to develop into canopy trees (Bond *et al.* 2003, Bond *et al.* 2012). The model for juvenile tropical savanna eucalypts (less than 1 m tall) was top kill without fire was only 2-4 % of the individuals but increased to 63% (non-sorghum ground layer savannas) to 83% (annual sorghum ground layer savannas) in early season burns. Late dry season burns resulted in 100 % topkill (Werner & Prior 2013). For the 228 shrub recruits of canopy trees in these four sites, many are killed within the first two years by fires or drought (Table 2 and 3). However, once established a minority of individual shrubs of *Melaleuca viridiflora, Petalostigma banksii, Erythrophleum chlorostachys, Eucalyptus platyphylla, Eucalyptus granitica, Corymbia clarksoniana, Corymbia citriodora, Grewia savannicola* and *Planchonia careya* were still alive after 30 years of monitoring and had survived up to six fires. *Allocasuarina torulosa* shrubs less than a metre tall were also observed resprouting after the hot fire in October 2014 at site 4. Three *Melaleuca viridiflora*, a species which does not form the canopy in these communities, persisted through six fires to become low subcanopy trees. In a re-sampling of 64 grassland and grassy woodland sites on Cape York Peninsula, Crowley & Garnett (1998) found that *Melaleuca viridiflora* had persisted at most sites and increased in 14% of the sites. Four out of 13 grassland sites, and three out of four mixed evergreen sites, were now dominated by *Melaleuca viridiflora* woodlands. Once *Melaleuca viridiflora* suckers or seedlings grow above the grass height, without fires, they will rapidly recruit to the subcanopy where they are resistant to most fires. Crowley *et al.* 2009 found that storm-burns (hot late season fires) were the most effective at preventing this process. This study casts no light on the influence of storm burns on seedling germination or recruitment. However, it is likely that seedlings would be killed by fires in the first year or so after germination (Fensham & Fairfax 2006). If so, then the fires following a heavy or extended wet season will be particularly important for minimizing seedling recruitment

The predicted annual height increment of juvenile trees was 16 cm in the Northern Territory, although it could vary from 29.4 cm to 12.5 cm/year with species. The transition rate from a 1m juvenile to sapling size ranged from 14 -22% depending on fire frequency and season. (Werner & Prior 2013). However, in this study none of the 228 individual shrubs of canopy species managed to break through the fire recruitment trap to become canopy trees over the 30 years of monitoring. An individual *Corymbia citriodora* seedling recruited to site 3 probably in 1999 during two consecutive wetter years with no subsequent fires. It was first measured in May 2001 as a 5 m tall sapling and grew rapidly (66.7 cm/year) to reach 7 metres in 2004 before being burnt in 2005 and reset as a shrub 1.85 metres tall. Since that time, it survived three more fires but has never been taller than 3.0 metres. The individual was not present at the June 2020 sampling so presumably was killed in the 2019 fire. An individual *Eucalyptus platyphylla* seedling recruited in site 2 post 1993 and was recorded as a shrub 1.2 m tall in 2001 and survived three fires as a shrub before reaching a low tree of 4.5 m in 2013, 5 m in 2014, 7 m in 2015 (surviving fires in 2014 and 2016) to be 7m tall in May 2018 before presumably dying in the 13 September 2018 fire. In the two years 2013-2015, this individual grew at 125 cm/year. (Figure 14)

Russell-Smith *et al.* (2019) report almost total fire suppression of juvenile trees from 32 sites in Litchfield National Park with only one eucalypt (growing at 20 cm/year) attaining a height >5m out of 819 juvenile trees. Lawes *et al.* (2011) found top kill across 19 species of subadults trees in northern Australia was correlated with absolute bark thickness, rather than stem height as suggested by Bond *et al.* 2012. The probability of a subadult not being top killed by a fire is dependent on it reaching a minimum height and particularly bark thickness, whereby it can survive the fire. The minimum height is dependent on the fire season and amount of fuel available (Werner & Prior 2013)

Hence across the four sites there was a nett loss in the number canopy trees, over the 30 period, with several canopy trees lost through gradual canopy decline (sites 1, 2 and 3) and two directly in hot fires. There was no replacement of these canopy trees by recruits or low trees escaping the fire trap to move towards the canopy during the 30-year period. There was a gradual increase in the number of non-canopy shrubs in sites 1, 2 and 3, both ephemeral seed regenerators and a range of species that were able to persist through repeated fires. *Jacksonia thesioides, Lamprolobium fruticosum* and *Acacia leptostachya* were short-lived, low fire-resistance shrubs that persisted at site 2 through adopting a rapid lifecycle and prolific seeding. It appears a fire in August 2000 may have created the opportunity for these species that were common in the nearby area to establish at the site by removing grass competition, and the regular fires allowed them to persist at the site.

Non-native species

There was also an exponential increase in density of the non-native *Stylosanthes scabra* at the *Eucalyptus platyphylla and Eucalyptus granitica* sites (Fig. 17). It is not clear what conditions allowed the proliferation of *S. scabra* post 2013, which had been recorded in 2000 in site 3, and 2001 in 1 and 2 (Neldner & Butler 2021), however all sites experienced two drier years after a very wet year in period in 2011-12. An increase in density of *S. scabra* at Brooklyn Station, 50 kilometres north of Mareeba, has been reported by Kemp & Kutt (2020) after the removal of domestic stock. *S. scabra* is a woody erect leguminous shrub from South America (Edye 1997) which may cause adverse environmental effects by outcompeting perennial grasses and promoting undesirable dicot weeds (Jones *et al.* 1997), as well as causing increased risks of soil erosion, soil acidification and fungal attack on the legume (McIvor *et al.* 1996). While fire kills above ground parts of *S. scabra* plants they may regrow from root tissue as much as 38cm below the soil surface and new individuals are able to germinate from the first rains from seed that has been softened by fire (Gardiner 1980, ACIAR 2020). High densities of *S. scabra* may dramatically change the composition of shrub and ground layer and it may be very difficult to reverse this dominance (Jones *et al.* 1997;

Cooksley & Quirk 1999). Orr (2010) found strategic seasonal grazing may reverse this process but requires average to good rainfall and five to eight years with careful grazing management to achieve. The rapid increase in *S. scabra* had not significantly impacted on the ground layer cover or composition up until the May 2021 sampling, although high densities are known to negatively impact ground layers and further monitoring is required to assess its future impact.

Conclusions

In four north Queensland eucalypt communities experiencing highly seasonal rainfall typical of the tropical savannas, over the 30 years there were seven dry years of rainfall (<60% mean annual rainfall) and eight wet years (>150% mean annual rainfall). There were up to eight fires and periods of light grazing by domestic stock at each site, apart from Site 1. Over the 30 years of this study, even though several individuals from a variety of species persisted through up to eight fires, and three *Melaleuca viridiflora* individuals developed to be low subcanopy trees, there were no individuals that survived to become canopy trees. There was general increase in the number of non-canopy species shrubs but a concerning loss in canopy trees, with no successful replacement. The spatial extent of this phenomena needs to be investigated, as it has the potential to destabilise the savanna structure and is a potential indicator of an ecosystem under stress. There was also a concerning increase in the non-native legume *Stylosanthes scabra* density at two sites since 2014, although it had not significantly impacted on the ground layer up until the May 2021 woody sampling. This three decade study of the woody components of tropical savannas records a decline in canopy density, a lack of canopy recruitment and a dramatic increase in *S. scabra* which are symptoms of potential decline in vegetation condition.

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References

Accad, A., Neldner, V.J., Kelley, J.A.R., Li, J. & Richter, D. (2021) *Remnant Regional Ecosystem Vegetation in Queensland, Analysis 1997-2019*. Queensland Department of Environment and Science: Brisbane. https://www.qld.gov.au/environment/plants-animals/plants/ecosystems/remnant-vegetation/

Addicott, E.P. & Newton, M. (eds.) (2012) Technical Descriptions of Regional Ecosystems of Einasleigh Uplands, (May 2012) (Queensland Herbarium, DSITI: Brisbane).

Allan G., Dyer R., Johnson A., Russell-Smith, J. & Yates C. (2001) Monitoring fire regimes. In: *Savanna burning - understanding and using fire in northern Australia* (Eds R. Dyer, P. Jacklyn, I. Partridge, J. Russell-Smith and D. Williams) pp. 102-21. Tropical Savannas CRC, Darwin.

Archer, S. (1995) Tree-grass dynamics in a *Prosopis*-thorn scrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience* 2: 83-99.

Australian Government (2022) Digital Earth Australia Hotspots http://sentinel.ga.gov.au/ (Accessed 28/06/2022).

Australian Centre for International Agricultural Research (ACIAR) (2020) *Stylosanthes scabra*. Tropical Forages Fact Sheet https://www.tropicalforages.info/text/entities/stylosanthes_scabra.htm (Accessed 6/1/2021)

Baker, P.J. & Bunyavejchewin, S. (2006) Suppression, release and canopy recruitment in five tree species from a seasonal tropical forest in western Thailand. *Journal of Tropical Ecology* 22: 521-529.

Bergstrom, D.M., Wienecke, B.C., van den Hoff, J., Hughes, L., Lindenmayer, D.B., Ainsworth, T.D., Baker, C.M., Bland, L. & Bowman, D.M.J.S. (2021) Combating ecosystem collapse from the tropics to the Antarctic. *Global Change Biology* 2021; 00:1-12. DOI: 10.1111/gcb.15539

Bond, W.J., Cook, G.D. & Williams, R.J. (2012) Which trees dominate in savannas? The escape hypothesis and eucalypts in Northern Australia. *Austral Ecology* 37: 678-685.

Bond W. J. & Midgley G. F. (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* 16: 45–51.

Bond, W.J., Midgley, G.F. & Woodward, F.I. (2003) What controls South African vegetation – climate or fire? *South African Journal of Botany* 69: 79–91.

Bond, W.J. & Van Wilgen, B.W. 1996. *Fire and Plants*. Population and Community Biology series 14. Chapman & Hall, London.

Brown, G.K. & Bostock, P.D (eds) (2020) Census of the Queensland Flora 2019. Queensland Herbarium, Department of Environment and Science, Brisbane. https://www.qld.gov.au/__data/assets/pdf_file/0028/67447/qld-flora-census.pdf

Bowman, D. M. J. S. & Fensham, R. J. (1991) Response of a monsoon forest-savanna boundary to fire protection, Weipa, northern Australia. *Australian Journal of Ecology* 16: 111-18.

Bowman, D.M.J.S. & Panton, W.J. (1995) Munmarlary revisited: Response of a north Australian *Eucalyptus tetrodonta* savanna protected from fire for 20 years. *Australian Journal of Ecology* 20**:** 526-31.

Bowman, D.M.J.S., Wilson, B.A. & Hooper, R.J. (1988) Response of *Eucalyptus* forest and woodland to four fire regimes at Munmarlary, Northern Territory. *Journal of Ecology* 76: 215-32.

Burrows, W.H., Henry, B.K., Back P.V., Hoffmann M. B., Tait, L.J., Anderson, E.R., Menke N., Danaher, T., Carter, J.O. and McKeon G.M. (2002) Growth and carbon stock change in eucalypt woodlands in northeast Australia: ecological and greenhouse sink implications. *Global Change Biology* 8: 769-784.

Clarkson, J.R. & Kenneally, K.F. (1988) The floras of Cape York and the Kimberleys: a preliminary comparative analysis. *Proceedings of the Ecological Society of Australia* 15: 259-66.

Chuvieco, E., Giglio, L. & Justice, C. (2008) Global characterization of fire activity: towards defining fire regimes from Earth observational data. *Global Change Biology* 14: 1488-1502.

Cooksley, D.G. & Quirk, M.F. (1999) Restoring perennial grasses to a stylo-dominant pasture. *Proceedings of the VI International Rangeland Congress*, Townsville. pp. 282– 283.

Crowley, G.M. and Garnett, S.T. (1998) Vegetation change in the grasslands and grassy woodlands of east-central Cape York Peninsula, Australia. *Pacific Conservation Biology* 4: 132-48.

Crowley, G.M., Garnett, S.T. and Shephard, S. (2009) Impact of storm-burning on *Melaleuca viridiflora* invasion of grasslands and grassy woodlands on Cape York Peninsula, Australia. *Austral Ecology* 34: 196-209.

Edye, L.A. (1997) Commercial development of *Stylosanthes* pastures in northern Australia. 1. Cultivar development within *Stylosanthes* in Australia. *Tropical Grasslands* 31: 503-508.

Fensham, R. J., (1990) Interactive effects of fire frequency and site factors in tropical *Eucalyptus* forest near Darwin, northern Australia. *Australian Journal of Ecology* 15: 255-66.

Fensham, R. (2012) Fire regimes in Australian tropical savanna: perspectives, paradigms and paradoxes. In Flammable Australia: Fire Regimes, Biodiversity and Ecosystems in a Changing World. Eds R.A. Bradstock, R.J. Williams and A.M. Gill, CSIRO Publishing, Melbourne, pp. 173 -194.

Fensham, R.J. and Bowman, D.M.J.S. (1992) Stand structure and the influences of overwood on regeneration in tropical Eucalypt forest on Melville Island. *Australian Journal of Botany* 40: 335-352.

Fensham, R.J., Fairfax, R.J. & Archer, S. (2005) Rainfall, land-use and woody vegetation cover change in semi-arid Australian savanna. *Journal of Ecology* 93: 596-606.

Fensham, R.J. & Holman, J.E. (1999) Temporal and spatial patterns in drought related tree dieback in Australian savanna. *Journal of Applied Ecology* 36: 1035-1050.

Fox, I.D., Neldner, V.J., Wilson, G.W., & Bannink, P.J. (2001) The vegetation of the Australian tropical savannas. Environmental Protection Agency, Brisbane.

Gardner, C.J. (1980) Tolerance of perennating *Stylosanthes* plants to fire. *Australian Journal of Experimental Agriculture and Animal Husbandry* 20: 587-593.

Hnatiuk, R.J., Thackway, R. & Walker, J. (2009) Vegetation. In *Australian Soil and Land Survey Field Handbook.* Third edition. (National Committee on Soil and Terrain) CSIRO publishing: Melbourne, pp. 73-125.

IPCC (2014) Climate Change 2014: Synthesis Report: summary for policymakers (P.K. Pachauri and L.A. Meyer, Eds.). IPCC, (Geneva, Switzerland) https://www.ipcc.ch/site/assets/uploads/2018/05/SYR_AR5_FINAL_full_wcover.pdf

Jeffrey, S.J., Carter, J.O., Moodie, K.M & Beswick, A.R. (2001) Using spatial interpolation to construct a comprehensive archive of Australian climate data. *Environmental Modelling. Software* 16, 309-30. https://www.data.qld.gov.au/dataset/silo-climate-database

Jones, R.J., McIvor, J.G., Middleton, C.H., Burrows, W.H., Orr, D.M. & Coates, D.B. (1997) Stability and productivity of *Stylosanthes* pastures in Australia. 1. Long-term botanical changes and their implication in grazed *Stylosanthes* pastures. *Tropical Grasslands* 31: 482-493.

Kemp, J.E. & Kutt, A.S. (2020) Vegetation change 10 years after cattle removal in a savanna landscape. *The Rangeland Journal* 42: 73-84. https://doi.org/10.1071/RJ19092

Lacey, C.J. & Whelan, P.I. (1976). Observations on the ecological significance of vegetative reproduction in the Katherine-Darwin region of the Northern Territory. *Australian Forestry* 39:131-139.

Lawes, M.J., Richards, A., Dathe, J. & Midgley, J.J. (2011) Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna of northern Australia. *Plant Ecology* 212: 2057-2069.

Lawes, M.J., Crisp, M.D., Clarke P.J., Murphy B.P., Midgley, J.J., Russell-Smith, J., Nano, C.E.M., Bradstock, R.A., Enright, N.J., Fontaine J.B., Gosper, C.R. & Woolley, L. (2022) Appraising widespread resprouting but variable levels of postfire seeding in Australian ecosystems: the effect of phylogeny, fire regime and productivity. *Australia Journal of Botany* 70:112-130. https://doi.org/10.1071/BT21110

Lehmann, C.E.R., Prior, L.D. & Bowman, D.M.J.S. (2009a) Fire controls population structure in four dominant tree species in a tropical savanna. *Oecologia* 161: 505-515.

Lehmann, C.E.R., Prior, L.D. & Bowman, D.M.J.S. (2009b) Decadal dynamics of tree cover in an Australian tropical savanna. *Austral Ecology* 34: 601-612.

McIvor, J.G., Noble, A.D. and Orr, D.M. (1996) Review of stability and productivity of native pastures oversown with tropical legumes. *Northern Australia Program Occasional Publication No. 1*. Meat and Livestock Australia Ltd, North Sydney.

Midgley, J.J., Lawes, M.J. & Chamaille-Jammes, S. (2011) Turner Review No. 19. Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Australian Journal of Botany* 58: 1-11.

Menaut, J-C. Grignoux, C., Prado, C. & Clobert, J. (1990) Tree community dynamics in a humid savanna of the Cote-d'Ivoire: modelling the impacts of fire and competition with grass and neighbours. *Journal of Biogeography* 17: 471-482.

Murphy, B.P., Liedloff, A.C. & Cook, G.D. (2015) Does fire limit tree biomass in Australian savannas? *International Journal of Wildland Fire* 24**:** 1-13.

Neldner, V. (2021) Seasonal changes in ground flora composition and cover in Queensland tropical woodlands. Version 1.0.0. Terrestrial Ecosystem Research Network (TERN). dataset. https://doi.org/10.25901/0jtn-qr55

Neldner, V.J. & Butler, D.W. (2021) Stability in the ground layer communities of tropical eucalypt woodlands of northern Queensland. *Australian. Journal of Botany* 69: 85-101.

Neldner, V.J., Fensham, R. J., Clarkson, J. R. & Stanton, J. P. (1997) The natural grasslands of Cape York Peninsula, Australia: Description, distribution, and conservation status. *Biological Conservation* 81: 121-36.

Neldner, V.J., Kirkwood, A.B. & Collyer, B.S. (2004) Optimum time for sampling floristic diversity in tropical eucalypt woodlands of northern Queensland. *Rangeland Journal* 26: 190-203.

Neldner, V.J., Wilson, B.A., Dillewaard H.A., Ryan, T.S., Butler, D. W., McDonald, W.J.F., Addicott, E.P. & Appelman, C.N. (2020) Methodology for Survey and Mapping of Regional Ecosystems and Vegetation Communities in Queensland. Version 5.1. Queensland Herbarium, Queensland. Department of Environment and Science, Brisbane.

Orr, D.M. (2010) Managing the grass-legume balance in *Stylosanthes scabra* cv. Seca pastures in central Queensland. *Tropical Grasslands* 44, 174–183. bit.ly/2wUxLx5

Prior, L.D., Brook, B.W., Williams, R.J., Werner, P.A., Bradshaw, C.J.A. & Bowmann, D.M.J.S. (2006) Environmental and allometric drivers of tree growth rates in a north Australian savanna. *Forest Ecology and Management* 234: 164-180.

Queensland Government (2021) Fire Scar Mapping. Statewide Monitoring Programs. https://www.qld.gov.au/environment/land/management/mapping/statewide-monitoring/firescar/firescar-explained

Queensland Herbarium (2021) Regional Ecosystem Description Database (REDD) Version 12 (March 2021). (Department of Environment and Science: Brisbane) http://www.ehp.qld.gov.au/ecosystems/biodiversity/regional-ecosystems/index.php

Russell-Smith J. (2013) Three Parks Savanna Fire-effects Plot Network: Plot-based Vegetation Sampling Data, Kakadu National Park, Northern Territory, Australia, (Long Term Ecological Research Network) Parks Australia, Australian Government Department of the Environment. Available at http://www.ltern.org.au/knb/metacat/datalibrarian.73.34/html

Russell-Smith J., Evans, J., Macdermott, H., Brocklehurst, P. Schatz, J., Lynch, D, Yates, C. & Edwards, A. (2019) Tree recruitment dynamics in fire-prone eucalypt savanna. *Ecosphere* 10 (3) article e02649.

Scholes, R.J. & Archer, S.R. (1977) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28: 517 - 44.

Schultz, N.L., Reid, N., Lodge, G. & Hunter, J.T. (2014) Seasonal and interannual variation in vegetation composition: Implications for survey design and data interpretation. *Austral Ecology* 39: 755-766.

Setterfield, S.A. (2002) Seedling establishment in an Australia tropical savanna: effects of seed supply, soil disturbance and fire. *Journal of Applied Ecology* 39: 949-59.

Specht, R.L. (1970) Vegetation. *In: The Australian environment* (4th edition). (Ed G.W. Leeper) pp. 44-67. CSIRO & Melbourne University Press.

Specht, R.L. (1981) Foliage projective cover and standing biomass. *In: Vegetation classification in Australia* (Eds A.N. Gillison & D.J. Anderson) pp. 10-21. CSIRO & Australian National University Press, Canberra.

Walker, B.H., Ludwig, D., Holling, C.S. & Peterman, R.S. (1981) Stability of semi-arid savanna grazing systems. *Journal of Ecology* 69: 473-498.

Walker, J. & Hopkins, M.S. (1990) Vegetation. *In: Australian soil & land survey field handbook* (Eds R.C. McDonald, R.F. Isbell, J.G. Speight, J. Walker & M.S. Hopkins) pp. 58-86. Second edition. Inkata Press, Melbourne.

Werner, P.A. (2012) Growth of juvenile and sapling trees differs with both fire season and understory type: trade-offs and transitions out of the fire trap in an Australian savanna. *Austral Ecology* 37: 644-657.

Werner, P.A. & Prior, L.D. (2013) Demography and growth of subadult savanna trees: interactions of like history, size, fire season, and grassy understory. *Ecological Monographs* 83: 67-93.

Williams, P.R. (2000) Fire-stimulated rainforest seedling recruitment and vegetative regeneration in a densely grassed wet sclerophyll forest of north-eastern Australia. *Australian Journal of Botany* 48: 651-658.

Williams, P. R., Congdon, R.A., Grice, A.C. & Clarke, P.J. (2003a) Effect of fire regime on plant abundance in a tropical eucalypt savanna of north-eastern Australia. *Australian Journal of Ecology* 28: 327-38.

Williams, P. R., (2009) Contrasting demographics of tropical savanna and temperate forest eucalypts provide insight into how savannas and forest function. A case study using *Corymbia clarksoniana* from north- eastern Australia. *Austral Ecology* 34: 120-31.

Williams, R.J., Cook, G.D., Gill A.M. & Moore P.H.R. (1999) Fire regime, fire intensity and tree survival in a tropical savannas in northern Australia. *Australian. Journal of Ecology* 24: 50-9.

Williams, R.J., Woinarski, J.C.Z. & Andersen, A.N. (2003b) Fire experiments in northern Australia: contributions to ecological understanding and biodiversity conservation in tropical savannas. *International Journal of Wildland Fire* 12: 391-402.

Wilson, B.A. & Bowman, D.M.J.S. (1994) Factors influencing tree growth in tropical savanna: studies of an abrupt Eucalyptus boundary at Yapilika, Melville Island, Northern Territory. *Journal of Tropical Ecology* 10: 103-120.

Wilson, B.A., Brocklehurst, P.S., Clark, M.J. & Dickinson, K.J.M. (1990) Vegetation Survey of the Northern Territory, Australia. *Technical Report No.* 49 pp. 19-21. Conservation Commission of the Northern Territory, Australia.

Woinarski, J.C.Z., Risler, J. & Kean, L. (2004). Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical Eucalyptus open forest, Northern Territory, Australia. *Austral Ecology* 29: 156-176.

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