


# Dynamics of the ground layer communities of tropical eucalypt woodlands of northern Queensland

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**Abstract.** This paper presents insights from long-term monitoring into the dynamics of savanna plant species composition, specifically on the ground layer. Key questions are (1) how much variation is there from year to year in plant species abundance and composition? And (2) is there evidence of directional change in community composition? Five sites were located near Mareeba, north-eastern Australia, and sampled 18 times with fixed 500-m<sup>2</sup> plots at the annual peak of plant species richness over 23 years. The sites were located in eucalypt communities across an altitudinal range of 460 m. Sampling involved systematic searching of all plant species visible above ground. The results show variation from year to year among satellite herbaceous species, with more than 50% of grasses and forbs observed at a given site only being detected at half or fewer of the 18 samplings. Herbaceous composition did not show clear signs of directional change relative to inter-annual variability. Over the 23 years, there were three very dry periods and 4 very wet years. Rainfall variation affected total cover more than plant species composition or richness. Several fires and episodes of grazing affected ground cover but did not have a lasting impact on cover or diversity. The cover and composition of the ground layer is consistently dominated by the core perennial grasses *Themeda triandra* Forssk. and *Heteropogon triticeus* (R.Br.) Stapf, with many species collectively contributing minimally to the overall cover but significantly to richness. Many herb species are persistent long-lived perennials which do not appear above ground every year. The number of naturalised plants in the ground layer was consistently low. Overall, the ground layer communities appear to be very stable in these woodlands that have been burnt 3–5 times in 23 years. High inter-annual variability of subdominant species is consistent with other studies, and emphasises the need for replication in time in ecological sampling.

**Keywords:** species turnover, floristic diversity, vegetation, savannas, long-term monitoring, *Themeda triandra*, sampling, Einasleigh Uplands bioregion, Wet Tropics bioregion.

Received 3 February 2020, accepted 22 January 2021, published online 12 March 2021

Savannas dominate the globe in tropical areas where the climate is seasonally wet and dry. The vegetation generally consists of canopy layer of C<sub>3</sub> trees and a ground stratum dominated by C<sub>4</sub> grasses (Williams *et al.* 2017). Tropical savannas cover ~20% of land worldwide and 25% of Australia (Fox *et al.* 2001; Williams *et al.* 2017) (Fig. S1 of the Supplementary material). Although the magnitude of the drivers of tropical savannas vary across the world, water availability, temperature and fire are primary determinants of Australian savanna structure which is uniquely dominated by the family Myrtaceae, with soil nutrients and grazing being less influential (Bond and Van Wilgen 1996; Sankaran *et al.* 2005; Hirota *et al.* 2011; Lehmann *et al.* 2011, 2014). As savannas are predominately used for pastoralism and biodiversity conservation, there has been significant research into the effects of climate, soils, grazing and fire

management on the savanna structure, particularly tree–grass interactions (Lehmann *et al.* 2014; Archibald *et al.* 2020).

Tree populations in tropical savannas are frequently characterised by very few saplings but a large number of suppressed juvenile trees <1 m tall of indeterminate age that have survived as multi-stemmed shrubs or lignotubers. This situation has been reported for the savannas of north America e.g. Scholes and Archer (1997), Asia e.g. Baker and Bunyavejchewin (2006), Africa e.g. Bond and Midgley (2001) and Australia Lehmann *et al.* (2009), Andersen *et al.* (2003), Scott *et al.* (2012), Werner and Prior (2013), Freeman *et al.* (2017), and fire appears to be an important demographic driver. The ‘fire trap’ hypothesis suggests that woody recruits need to rapidly grow to escape the fire recruitment bottleneck if they are to develop into canopy trees, which

implies that suppressed juveniles are ‘caught’ within the trap (Bond *et al.* 2003, 2012).

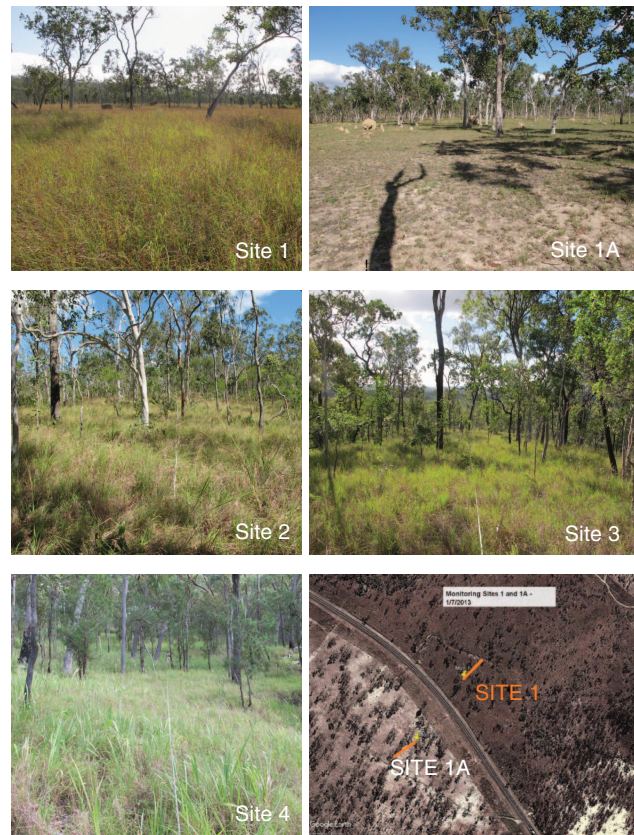
Long-term studies in Australian tropical savannas (e.g. Bowman *et al.* 1988; Bowman and Panton 1995; Andersen *et al.* 2003, Scott *et al.* 2009, 2012) have focused primarily on the dynamics of woody trees and shrubs and their responses to fire and herbivory (Williams *et al.* 2003; Midgley *et al.* 2010; Werner and Peacock 2019) rather than the larger pool of herbaceous species in the ground layer. Russell-Smith *et al.* (2003b) noted high levels of variation from year to year in ground layer savanna species composition, but few other published long-term observations exist to corroborate or extend that observation (Williams *et al.* 2003; Scott *et al.* 2012). Many of the ground flora species of the Australian open forest savannas are perennial with buds protected in a range of subterranean organs such as bulbs, corms, stem tubers or root tubers (Pate and Dixon 1982; Klimesvá and Klimes 2007). Tall grasses, some with flowering stalks to 2 m tall, proliferate during the wet season and often burn during the dry season in fires deliberately lit by land managers or ignited naturally by lightning strikes (Williams *et al.* 1999; Allan *et al.* 2001; Dyer *et al.* 2001). Others are annual species or herbaceous perennials that senesce during the dry season and are not always detected in field surveys (Rice and Westoby 1983; Taylor and Dunlop 1985; Pärtel 2014). Herbaceous species richness may not vary much from year to year, but there could be significant changes in species’ dominance and community composition, which can only be revealed through repeated observation through time (Ives *et al.* 2003; Benson and Picone 2009).

The aim of this study was to document temporal changes in the abundance of plant species in the ground layer of monsoonal savannas in northern Queensland. The ground layer is characterised by short statured plants and may include graminoids, forbs, sprawling vines, shrubs and seedlings or suckers of trees generally less than 100 cm tall (Neldner *et al.* 2020). The floristic composition of the ground layer is extremely important in savanna systems because more than half of plant species in savannas are herbaceous. We assess data on variation in ground layer species’ abundance over a 23-year period, including correlations with possible drivers such as rainfall variability, domestic grazing and sporadic fires, which are fundamental to understanding the global savanna biome.

## Methods

### Site settings

Five permanently marked sites were established within a 750-km<sup>2</sup> area of northern Queensland. All were in open forests and woodlands dominated by *Eucalyptus* spp. and *Corymbia* spp. (broad vegetation group 2 in Fox *et al.* 2001) and within 20 km of Mareeba in north-eastern Australia (Fig. 1, S1). There was significant variation between sites both in terms of the environmental conditions (landscape position, geology, and climate) and the dominant tree species. Each site occurred in a different regional ecosystem and across three different land zones (Queensland Herbarium 2019). The altitudinal range of the sites from 380 to 840 m above sea level, was associated with mean annual rainfall ranging from 997 to 1457 mm (Fig. S2 of



**Fig. 1.** Photos of the five study sites taken 26 May 2013. Sites 1 and 1A *Eucalyptus platyphylla* and *E. leptophleba* grassy open woodland, Site 2 *Corymbia clarksoniana* woodland with *Eucalyptus leptophleba*, *E. platyphylla* and *C. dallachiana*, Site 3 *Eucalyptus granitica* woodland with *Corymbia citriodora*, *C. clarksoniana* and *Erythrophleum chlorostachys*, and Site 4 *Eucalyptus reducta* and *Corymbia intermedia* open forest with *C. citriodora* and *E. granitica*. Note the reduced ground layer biomass in Site 1a which is grazed by cattle as compared to the nearby Site 1. This grazing effect is clearly seen along the fence line in the aerial photograph on 1 July 2013.

the Supplementary material). Details of the site characteristics, together with the frequency of fires and observations of grazing impacts are summarised in Table 1. Fig. 1 is photographs of the sites in 2013 and demonstrates clearly the grazing impact on the ground cover when comparing Sites 1 and 1A.

### Field sampling

This study is based on repeated samplings of five permanently marked locations. Sampling methods followed the standard for detailed vegetation survey sites utilised by the Queensland Herbarium (Neldner *et al.* 2020). In summary, a single 50-m transect was established by V. J. Neldner in November 1991 (1993 for Site 1A) at each site and permanently marked at both ends with steel pickets.

A previous 3-year seasonal study conducted on these sites in 1992–1994, confirmed that a late wet season sampling (early May) recorded the majority of the ground layer species (Neldner *et al.* 2004). This is different to winter-rainfall dominated temperate grassy woodlands in south-eastern

**Table 1. Location, annual rainfall, disturbance, sampling details and description of the five monitoring sites**

Sites 1–4 were sampled on 18 occasions for the Number of samplings when grazed category. Site 1A was sampled on 16 occasions. Evidence of grazing included faeces of domestic stock, hoof prints and eaten plant parts. For regional ecosystem and remnant extent in 2017, regional ecosystems are described in Queensland Herbarium (2019) and their 2017 remnant extent documented in Accad *et al.* (2019)

Site number	Tenure	Location of origin of site (Intergovernmental Committee on Surveying and Mapping 2014)	Elevation (m above mean sea level)	Mean annual rainfall (mm)	Number of samplings when grazed	Number of fires during sampling period	Regional ecosystem and remnant extent in 2017	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	997	0	1	9.5.9b; 20,949 ha	<i>Eucalyptus platyphylla</i> and <i>E. leptophleba</i> grassy open woodland (15–20 m tall) (BA 5 m <sup>2</sup> ha <sup>–1</sup> ) on depositional plain
1A	Leased grazing property	–16.854725, 145.38777	380	997	3	3	9.5.9b; 20,949 ha	<i>Eucalyptus platyphylla</i> and <i>E. leptophleba</i> grassy open woodland (15–20 m tall) (BA 5 m <sup>2</sup> ha <sup>–1</sup> ) on depositional plain
2	Grazing lease, Dinden State Forest	–16.970556, 145.568054	440	1300	5	5	7.11.21a; 12,185 ha	<i>Corymbia clarksoniana</i> woodland (14–20 m tall) (BA 12 m <sup>2</sup> ha <sup>–1</sup> ) with <i>Eucalyptus leptophleba</i> , <i>E. platyphylla</i> and <i>C. dallachiana</i> on lower slopes of metamorphic range
3	Davies Creek National Park	–16.999235, 145.563478	600	1257	0	5	9.11.4a; 26,949 ha	<i>Eucalyptus granitica</i> woodland (18–22 m tall) (BA 8 m <sup>2</sup> ha <sup>–1</sup> ) with <i>Corymbia citriodora</i> , <i>C. clarksoniana</i> and <i>Erythrophloeum chlorostachys</i> on ridge crest of metamorphic range
4	Grazing lease, Danbulla State Forest	–17.114449, 145.54194	840	1457	6	5	7.12.27a; 16,030 ha	<i>Eucalyptus reducta</i> and <i>Corymbia intermedia</i> open forest (22–25 m tall) (BA 18 m <sup>2</sup> ha <sup>–1</sup> ) with <i>C. citriodora</i> and <i>E. granitica</i> on upper slope of steep granite range

Australia where richness peaks in spring (Burrows 2004; Schultz *et al.* 2014). Ground layer sampling occurred on or near 1 May in 18 of the 23 years between 1992 and 2015. The 6 years when no sampling occurred were 1995, 1996, 2005, 2011, 2012 and 2014.

Projective foliage cover (PFC) of each ground layer species was visually estimated to the nearest 1% in ten 1-m<sup>2</sup> quadrats placed at 5-m intervals along the transect. The cover values for each species from the ten quadrats were averaged to provide a mean cover for each species at the site. In addition to the ten quadrats, all vascular plant species occurring within 5 m either side of the centre line (500-m<sup>2</sup> area) were recorded, with the majority vouchered at the Queensland Herbarium to address future taxonomic changes (Sparrow 2017). Plant nomenclature followed Brown and Bostock (2019). PFC of the tree canopy was recorded at each sampling using the line intercept method (Neldner *et al.* 2020). Visual estimates of cover have been shown to correlate highly with ground cover estimates derived by various more objectively repeatable methods including mapped areas, digital image analysis and point quadrat methods (Vanha-Majamaa *et al.* 2000; Murphy and Lodge 2002). One author (V. J. Neldner) provided the visual estimates of the actual cover values for all samplings, and hence reduced potential observer variability.

#### Data analysis

Data manipulation and statistical analyses were performed using R (ver. 3.0, see <http://www.r-project.org/>, accessed 1 February 2021). Ordination used the metaMDS routine from the R-package ‘vegan’ (ver. 2.0-8, see <https://cran.r-project.org/web/packages/vegan/index.html>), which was applied following square-root transformation of the percentage cover data. Regression was used to assess relationships between wet season rainfall, time since last fire in months, ground layer vegetation cover and species richness (number of species) (model structures are specified in results). Regression models were developed across all sites with the ‘lmer’ function from the R-package ‘lme4’ (ver. 1.1-26, see <https://cran.r-project.org/web/packages/lme4/index.html>; Bates *et al.* 2015) to assess evidence of effects across the whole dataset. Predictors were treated as fixed effects with ‘site’ as a random effect in all models. This model structure allowed intercepts to vary between sites but estimated a common parameter for the slope of the relationship between predictor and response. Results are generally presented at the individual site level as there is substantial between-site variation in many of the relationships. The sites clustered consistently together in the ordination, reinforcing the unique ground flora communities at each site. To summarise the influence of lifeform and longevity, the frequency of species are analysed as site × species sampling combinations, e.g. *Themeda triandra* in Sites 1, 1A, 2, 3, and 4 represent five combinations at each sampling.

Statistical significance of fixed effects were assessed by comparing models that included the particular fixed-effect with an appropriate ‘null’ model, containing only the random effect for sites, using maximum likelihood



estimation through the ‘ANOVA’ function in R. Because there was a clear effect of rainfall on total cover and species richness, the null models used to test the effect of time since fire on these two variables, include rainfall as well as the random effect for sites. Where the mixed regression models indicated significant effects, simpler linear models were used to examine relationships between variables at each site using the ‘lm’ function in R. The relationship between cumulative species richness and the number of times each site had been sampled was examined using standardised major axis regression to fit curves of the form  $\text{species number} \sim e^{\text{sample-effort}}$  with the R-package ‘smatr’ (ver. 3.4-8, see <https://cran.r-project.org/web/packages/smatr/index.html>; Warton *et al.* 2012).

## Results

### Species

A total of 218 vascular plant species, representing 45 families, was recorded in the ground layer across the site samplings (88 events, 18 years  $\times$  4 (of 5) sites, plus 16 years for Site 1A) and over the 23 years. The majority of the species were native (88.5%) and perennial (60.5%). Poaceae (44 species) and Fabaceae (30 species) were the dominant families in both richness and total cover. Statistical indicators of variability in the species cover and site composition are presented in Table S1 of the Supplementary material, and graphically presented in a pearl diagram for Site 1 as an example (Fig. 2). Similar diagrams for each site, indicating the cover of each species at each sampling are in Fig. S3 of the Supplementary material. Fig. 3 displays the frequency distribution of species (using species  $\times$  site  $\times$  sampling combinations) over the sampling period, which shows a familiar bimodal distribution. Many species particularly annual forbs only occur infrequently (satellite species), whereas there is a group of species, mostly perennial grasses that are always present (core species). Of the total of 218 species, only 15 occurred at all 5 sites (17 at 4, 22 at 3, 76 at 2, and 88 only at 1 site).

### Site grouping of the ground flora

The sites formed distinct clusters in the ordination of 88 ground layer samplings across the different sites over the 23 years (Fig. 4). Only three outlier samples fell outside their site clusters in the ordination. Two of these outliers were sampled soon after fire. The two sites on landforms underlain by metamorphic rocks (Land zone 11, Sites 2 and 3), whereas forming distinct groups, are more closely related to each other than the other three sites that occurred on different land zones. As expected the grazed and ungrazed sites in the same regional ecosystem (1 and 1A) on the depositional Land zone 5 are very closely related to each other, but samples from each of these two adjacent sites still formed distinct groups in the ordination. Site 4 which occurred on a granitic substrate (Land zone 12) and received the most annual rainfall formed a clearly distinct group. Interestingly, there is no sign of directional change through time in the composition of the ground layers at individual sites, as evidenced by the detailed ordination panels in Fig. 4b–d with year of sampling shown within each symbol.

### Species richness across sites

At all sites the number of non-native species was low (mean less than four species per site, Table 2). The number of all species was consistently highest at Site 2 (mean =  $48.3 \pm 9.1$  s.d.) and Site 3 (mean =  $53.2 \pm 8.6$  s.d.). These two sites, with medium or high mean rainfall and regular burning, also had the highest variability in richness and the largest number and cover of annual species (Table 2). They also had relatively low cover of the dominant perennial grasses *T. triandra* and *Heteropogon triticeus* (Table 3) compared to the other sites where perennial grasses made up 97% or more of the overall ground cover.

Site 4 received the highest rainfall and was regularly burnt and recorded a moderate species richness (mean =  $33.6 \pm 6.4$  s.d.) with the highest integrity of species recorded at each sample. Non-native species made up the lowest proportion of the species recorded (5.2%) of any of the sites. There was only a low number of annual species ( $7.2 \pm 2.9$  s.d.) recorded at each sampling.

The paired sites (1 and 1A) had the lowest overall richness per sampling  $29.1 \pm 5.9$  s.d. and  $26.4 \pm 5.1$  s.d. respectively. They also had the highest percentage of non-native species per sampling 13.4 and 15.2 respectively. In these sites, the proportion of annual species per sampling was the lowest 6.2 and 6.4 respectively.

### Total cover of ground layers

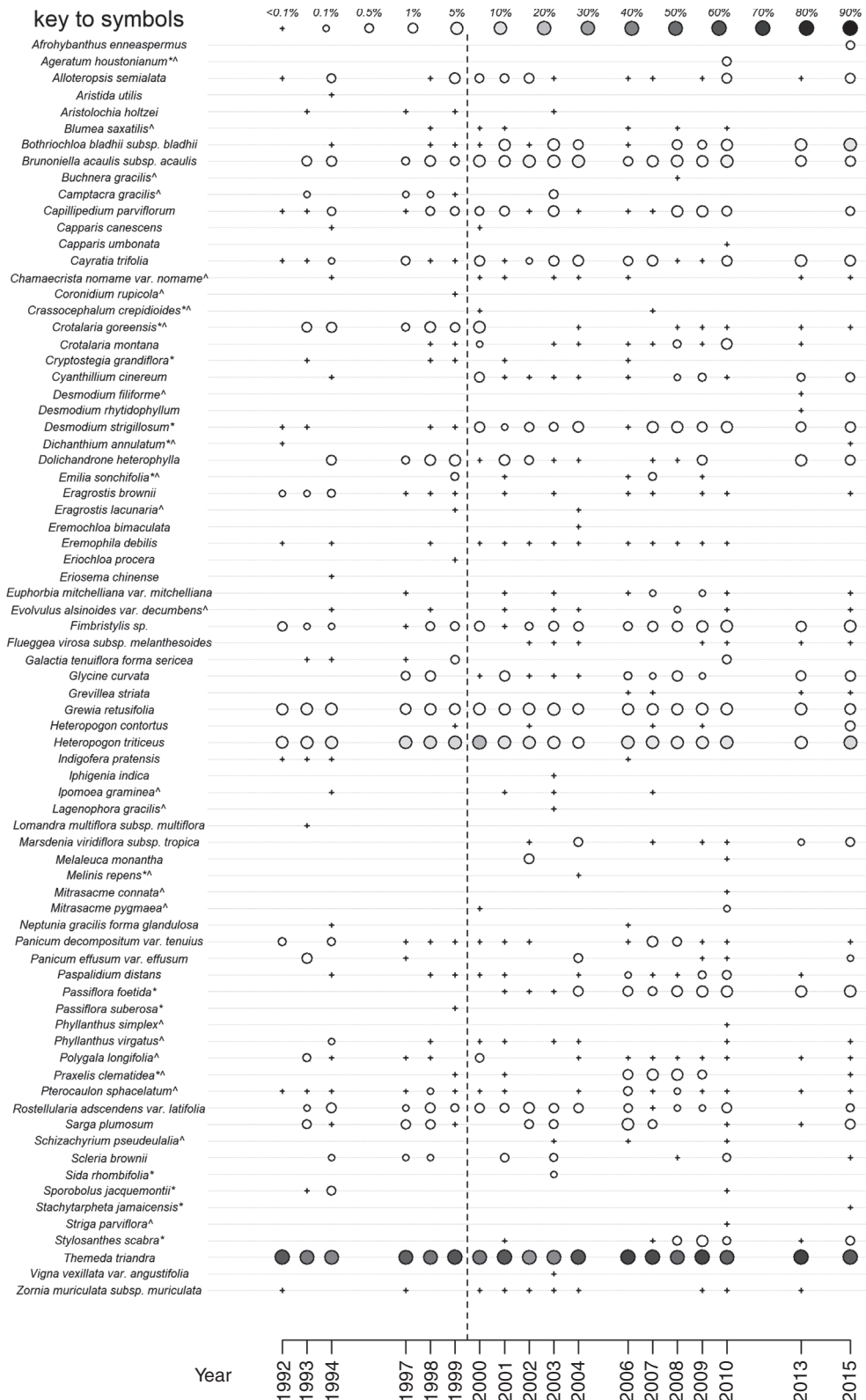
All sites had a total cover for the ground layer of more than 40% (sum of PFC for all species, averaged over the 18 samplings). Site 2 had the lowest mean cover (40.5%) and the driest site (Site 1) the highest (74.6%). The variation in total cover across all years was relatively low for all sites (s.d. ranging from 11.3 to 14.6% for Sites 1–4, with s.d. of 21.4 at the grazed Site 1A).

There was a positive linear relationship between the amount of rainfall received in the wet season and the cover of the ground layer. This relationship was most strongly apparent in Sites 1, 1A and 2, particularly when the sum of the previous two wet seasons were included (see Table 4; Fig. 5 and Fig. S4, S5 of the Supplementary material). Total ground cover and dominant grass species cover were the strongest vectors in two dimensional ordinations of the species composition data for each site. Canopy tree cover varied little and was not correlated with wet season rainfall (Fig. S6 of the Supplementary material) nor with ground cover (Fig. S7 of the Supplementary material).

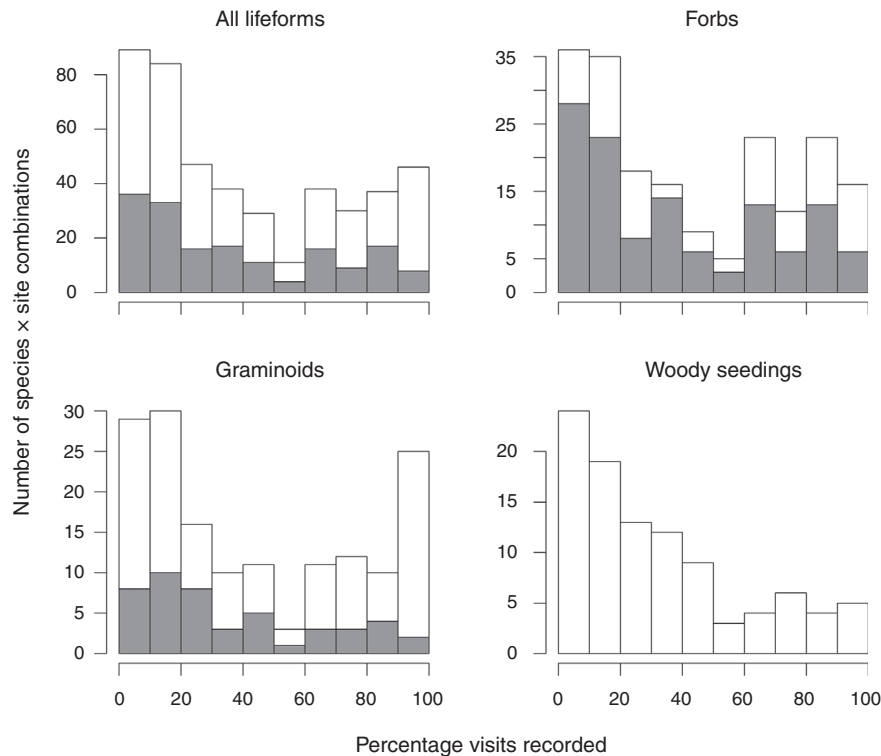
Annual species contributed only a minor proportion of the ground cover in the driest and wettest sites (Sites 1, 1A and 4; 1.9, 1.7 and 2.5 respectively), but their contribution was more substantial in mid-range rainfall sites (Sites 2 and 3; 27.2 and 18.0% respectively) (Table 3). The average total cover in the grazing paddock (Site 1A) was significantly lower than the ungrazed site nearby (Site 1) (Table 3). Site (1A) had the most variable total cover (s.d. 21.4.)

### Species richness over time

The cumulative species richness increased with successive samplings in all sites (Fig. 6). The exponent of the species–time relationship (i.e. the slope of the log-log linear



**Fig. 2.** Pearl diagrams of species present and cover over 23-year period for Site 1. The size of the circle represents the species cover up to a maximum size of 20% with the darker the fill in colour in the circle representing greater ground cover: a plus (+) denotes species present with negligible cover and the dotted line represents a fire at the site; a circumflex (^) denotes an annual species, whereas an asterisk (\*) denotes a non-native species.



**Fig. 3.** Frequency of recording of ground layer species, shown as bar graphs of site  $\times$  species combinations (e.g. *Themeda triandra* in Site 1, 1A, 2, 3, and 4 represent five combinations) over the 23 years and across all five sites. The grey part of the bar represents the number of annual species, whereas the remaining part represents perennial species.

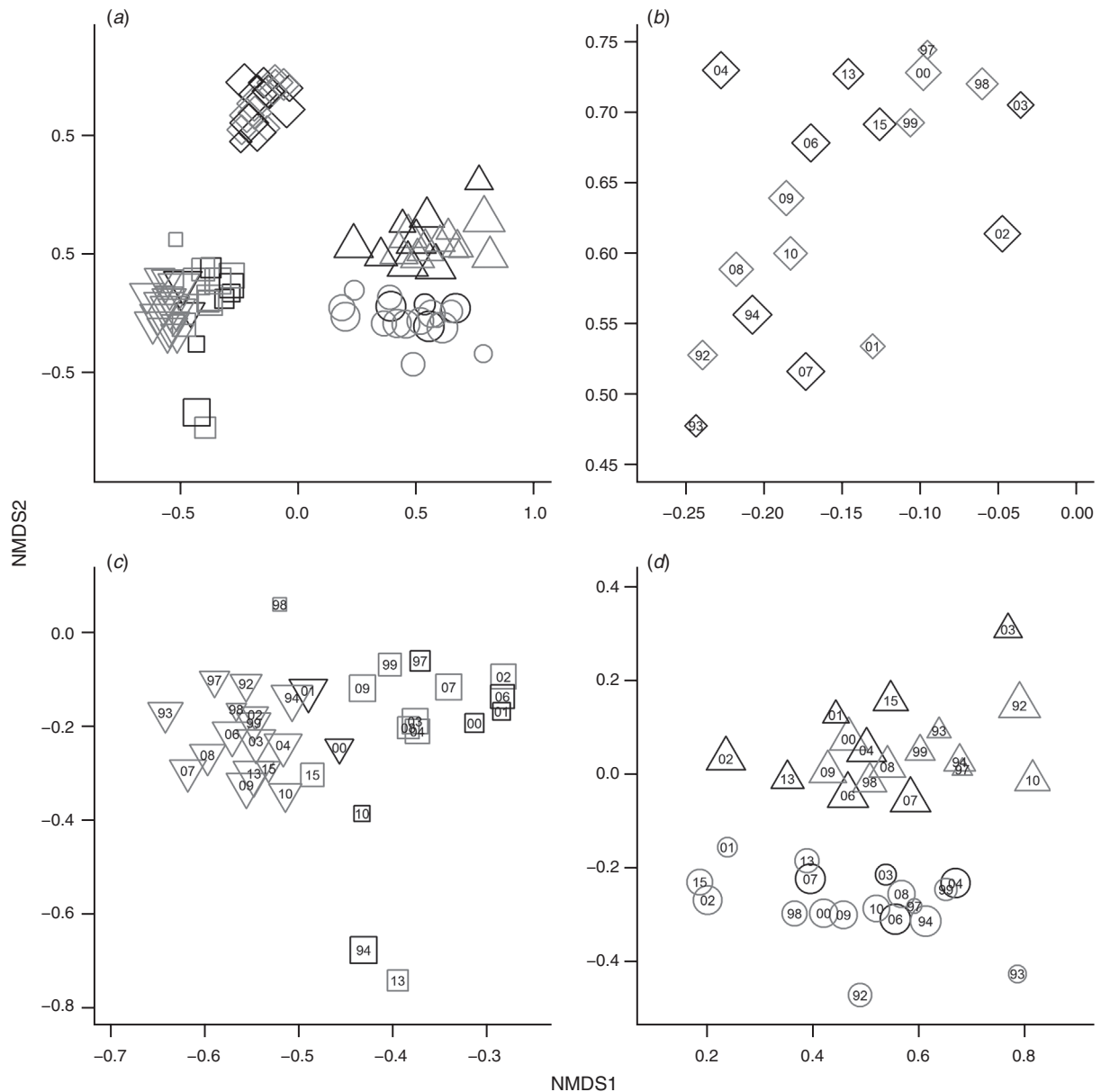
relationship between the natural logarithm of cumulative richness and the natural log of the number of ~annual samples recorded) ranged from 0.33 to 0.54, and was largest in the more depauperate, driest sites (Sites 1 and 1A). These sites also had high cover that was strongly dominated by perennial tussock grasses.

All sites are continuing to accumulate new species although the rate is relatively slower for the more diverse sites (2 and 3). Occasional additional species are recorded over time, e.g. *Ischaemum rugosum* was recorded for the first time on Site 1A in 2013, in a protected-from-grazing situation at the base of a termite mound.

At all sites except Site 2, the majority (>60%) of the species in the ground layer were encountered on more than half of the sampling occasions (Table 2). This pattern is broadly similar across graminoids, forbs and woody lifeforms across all sites. The species of shrubs and trees (which were included in the ground layer only as seedlings and small plants < 100 cm tall), however, were only rarely present (Fig. 3). The mid-rainfall site (Site 2) was the most diverse site overall, partly because of a greater number of shrub species present in the ground layer than other sites, but it also because of a greater number of annual species per sampling ( $\geq 21$ ). The percentage of species that were recorded at all of the 18 sampling occasions ranged from 5.8 to 12.5% (Sites 2 and 4 respectively).

#### Non-native species

The cover of non-native plants in the ground layer was relatively low both for number of species (11% of the overall flora recorded) and their overall contribution to ground cover (maximum of 5.1% of the ground cover) (Table 3). Of the non-native species, *Sporobolus jacquemontii*, *Lantana camara* and *Cryptostegia grandiflora* are the only species from the sites that are restricted invasive plants under the Queensland government *Biosecurity Act* 2014. The presence across sites and frequency of occurrence within sites of the 25 non-native species (11% of the overall flora) are listed in Table S2 of the Supplementary material. There was an average of four or fewer non-native species present at a sampling of any site (Table 2 and Table S2) with a maximum of eight species at any individual sampling, and at only one site (Site 1A). Seven species of non-native plants were recorded at every site at some sampling, while eight species were only ever recorded at a single site. Species from three families were recorded at four or more sites: the Asteraceae *Ageratum houstonianum*, *Emilia sonchifolia* and *Praxelis clematidea*; Fabaceae *Crotalaria goreensis*, *Desmodium strigillosum* and *Stylosanthes scabra*, and Poaceae *Melinis repens*. Comparing sites, the non-native species had their highest contribution to the ground layer,



**Fig. 4.** Ordination diagram of ground layer floras at five sites showing 88 recordings over 23 years of repeated sampling. (a) All sites, (b–d) show sections of the ordination in greater detail. Inverted triangle, Site 1; square, Site 1A; triangle, Site 2; circle, Site 3; diamond, Site 4. Numerals indicate year of sampling, e.g. '01' is 2001, symbol size is proportional to rainfall in the wet season before sampling, and symbols with black outlines indicate fire at the site within 24 months before sampling. MDS stress in 2-D (a) = 0.126.

**Table 2.** Summary of species richness in the ground layer for various lifeforms and native and exotic species at the five study sites

Site number	Total species of native vascular plants	Total species of non-native plants	Total number of native graminoid species	Total number of native forb species	Total number of native shrub species	Mean number of species per sample	s.d.	Mean number of annual species per sample	Mean number of non-native species per sample	Mean percentage of non-native species per sample	Percentage of species recorded >50% of samplings	Percentage of species recorded at every sampling
1	73	15	25	37	11	29.1	5.9	6.2	3.9	13.4	60.3	8.2
1A	66	13	31	24	11	26.4	5.1	6.4	4.0	15.2	65.2	6.1
2	120	13	43	56	21	51.3	9.1	21.4	3.3	6.8	52.1	5.8
3	106	9	32	54	20	54.8	8.6	21.9	2.9	5.5	69.5	7.6
4	75	9	25	40	10	33.6	6.4	7.2	1.6	5.2	72.2	12.5

**Table 3. A summary of mean cover values of perennial and annual ground layer species, two dominant grasses, and of exotic and of native species at each of the five study sites**

Means were calculated for 18 observations (16 at Site 1A) at each site over 23 years

Site number	Mean total cover of ground layer	s.d.	Mean cover of perennial species (percentage of total cover)	Mean cover of annual species (percentage of total cover)	Mean cover of <i>Themeda triandra</i> (percentage of total cover)	Mean cover of <i>Heteropogon triticeus</i> (percentage of total cover)	Mean cover of other native species (percentage of total cover)	Mean cover of non-native species (percentage of total cover)
1	77.7	11.3	76.2 (98)	1.5 (2)	53.3 (69)	8.1 (10)	13.4 (17)	2.9 (4)
1A	59.1	21.4	58.1 (98)	1.0 (2)	42.1 (71)	2.5 (4)	10.6 (18)	4.0 (7)
2	43.8	13.3	31.9 (73)	11.9 (27)	20.6 (47)	2.0 (5)	20.4 (47)	0.8 (2)
3	59.3	12.2	48.8 (82)	10.7 (18)	31.3 (53)	3.7 (6)	22.3 (38)	0.6 (1)
4	67.0	14.6	65.3 (97)	1.7 (3)	36.2 (54)	1.1 (2)	30.4 (45)	0.3 (0.4)

**Table 4. Summary statistics for models used in analysis**

Model	Null model	Null model deviance	Model deviance	Chi-Square	P
richness ~cover + 1 site	richness ~1 site	612.81	598.8	14.01	0.0009
richness ~rain_1wet + 1 site	richness ~1 site	612.81	601.6	11.23	0.004
richness ~rain_2wets + 1 site	richness ~1 site	612.81	601	11.84	0.003
richness ~rain_2wets + time_since_fire + 1 site	richness ~rain_2wets + 1 site	601	599.6	1.38	> 0.05
cover ~rain_1wet + 1 site	cover ~1 site	740.85	735.94	4.91	> 0.05
cover ~rain_2wets + 1 site	cover ~1 site	740.85	723.68	17.18	0.0002
cover ~rain_2wets + time_since_fire + 1 site	cover ~rain_2wets + 1 site	723.68	709.58	14.09	0.003

both in mean number and total cover, in the most regularly grazed site (1A) (Table 3).

During the 23 years the sites have been invaded by *P. clematidea*, a non-native species that has rapidly expanded its range in the last two decades and is on the Australia Alert List for Environmental Weeds (Laidlaw 2013). It was first recorded in the sites in 1999 (Sites 1A and 4), 2000 (3), 2006 (1) and 2007 (2). It has continued to persist in disturbed areas near the sites, and appeared to be increasing in cover from 2006 to 2008 at Sites 1 and 1A. However, after this initial invasion its subsequent cover and persistence at sites was very low. It was only recorded at Sites 2 and 4 in 2013 and 2015.

*Passiflora suberosa*, which was first recorded at Site 1 in 2001 and 1A in 2008, is persisting and increasing in cover (maximum cover of 2.5%) in the ungrazed Site 1. Its ability to sprawl over the top of the dense *T. triandra* sward allows it to compete effectively for light at this ungrazed site. *Passiflora foetida* has not persisted in the adjacent grazed Site 1A, only being recorded in 2008 and 2010.

### Grazing

Three sites (1A, 2, and 4) had evidence of domestic grazing (presence of faeces, hoof prints and eaten plant parts) on several occasions (Table 1). A comparison of the paired sites in the low-rainfall area (1 and 1A) suggests that grazing reduced the mean species richness (Table 2), the

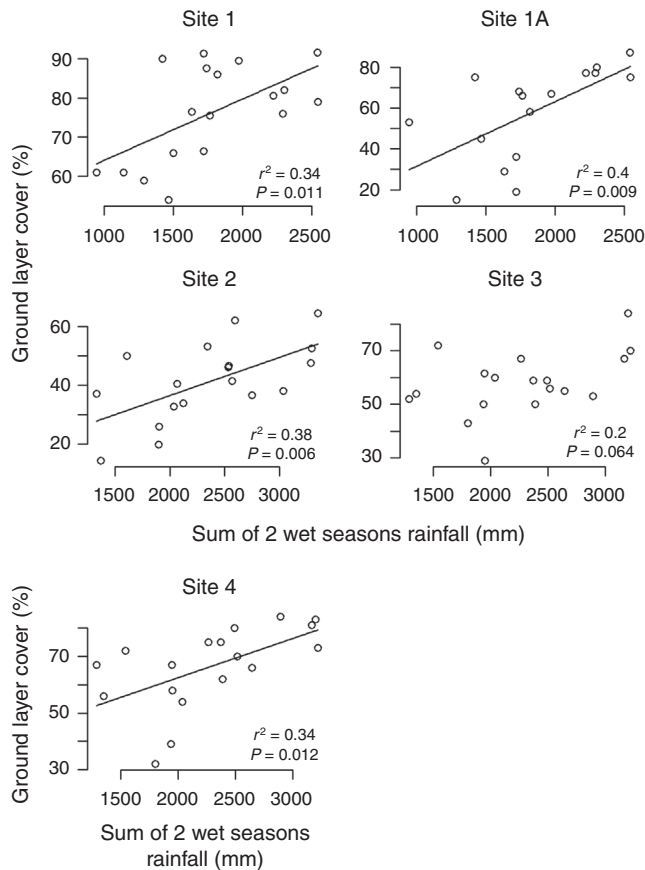
mean ground cover and ground cover of the dominant perennial grasses (Table 3). There were 13 non-native species at both sites (none dominant), with increased cover of *S. scabra* in the grazed site (1A) site in the 2013 and 2015 samplings.

### Fire

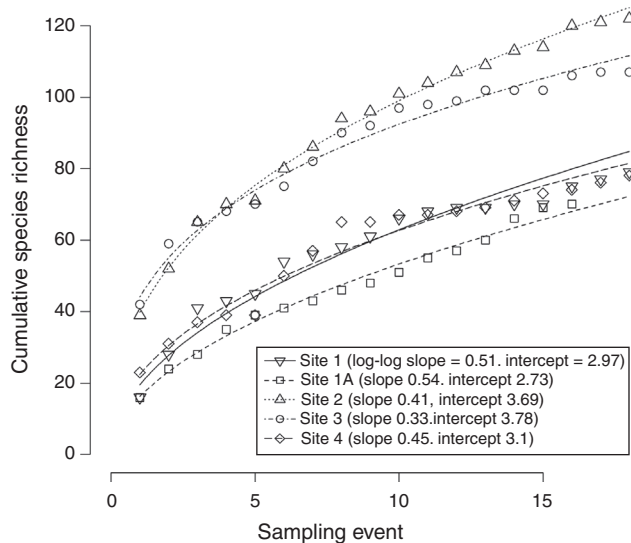
Low intensity fires that burnt the ground and shrub layer occurred in all sites, with Site 1 only being burnt once in September 1999 (Fig. S3). The fires generally occurred in the dry season from July to November, with the fire intensity increasing with fuel load, monthly temperature and prevailing local weather conditions. An intense fire in Site 4 in October 2014 scorched the canopy of trees, felled a canopy tree on the site and burnt all the subcanopy *Allocasuarina torulosa* trees. Sites 2 and 4 were grazing leases on state forest and Site 3 was in a national park. These sites had active fire management which aimed to burn each area every 3 years with the drier areas burnt in June and the wetter ones as late as August (R. Miller, pers. comm.). Five fires occurred every 2–5 years in Sites 2 and 3, whereas the fire interval for Site 4 ranged from 1 to 10 years. In the grazed property, three fires occurred at an interval of 5–7 years, although the adjacent road reserve only burnt once.

Time since fire had less influence on total ground cover or dominant species than the magnitude of the wet season, but was greatest at the mid-rainfall sites (2 and 3) where each had





**Fig. 5.** Ground cover (%) compared with the sum of the two previous wet season rainfall for five sites over 23 years. Linear regression lines fitted to data where  $P < 0.05$ .

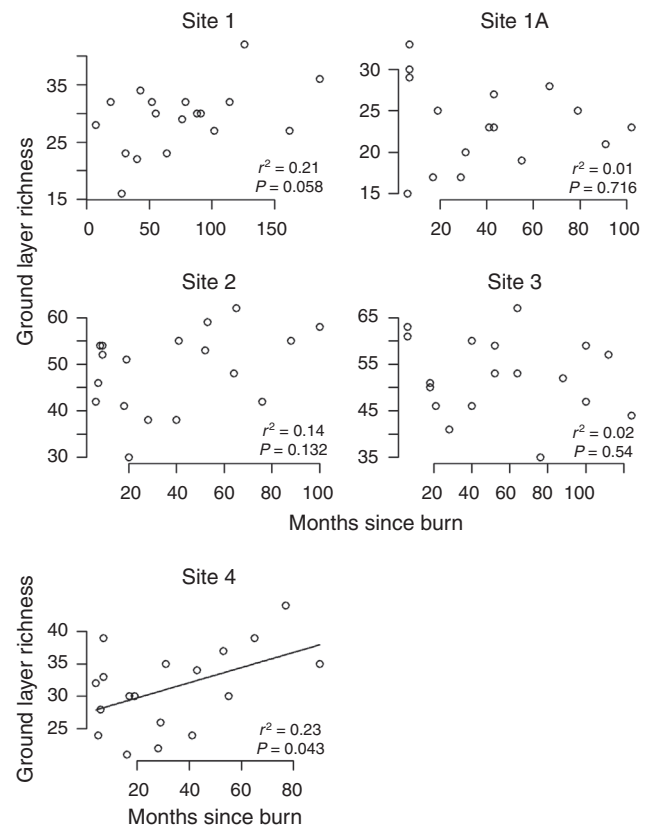


**Fig. 6.** Species-time response curves for the five sites over 23 years of sampling.

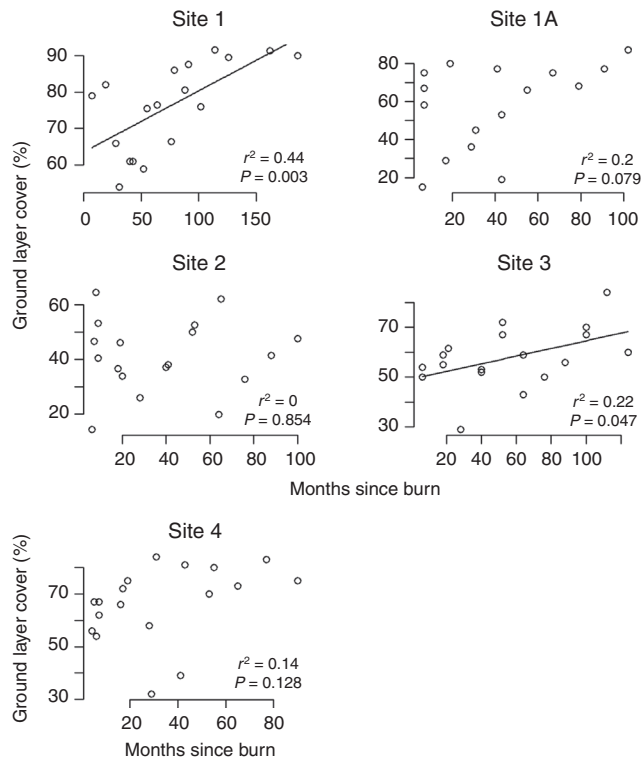
experienced five fires during the 23 years of the study (Fig. S8 of the Supplementary material), suggesting that fire *per se* may be a strong factor in determining species composition. However species richness was only correlated with months since fire for Site 4 (Fig. 7). The number of months since fire was positively correlated with ground cover for Sites 1 and 3 only (Fig. 8).

#### Species richness correlations

Statistical parameters for the mixed regression model analysing correlations of fire and rainfall and total species cover, and the effects of all three as drivers of richness are summarised in Table 4. Ground layer species richness was positively correlated with ground layer cover, with the clearest relationship in Sites 2 and 4 (Fig. 9). Within each site, there was a positive correlation, although across sites those with lower average cover (Sites 2 and 3) tended to have higher species richness. There was a weak positive relationship between species richness and mean annual rainfall for Site 2 (Fig. S9 of the Supplementary material). Further, when rainfall in consecutive wet seasons was used as the explanatory (predictor) variable, the relationship was slightly stronger for Sites 2 and 4 (Fig. 10).



**Fig. 7.** Species richness compared with months since last fire for five sites over 23 years. Linear regression lines fitted to data where  $P < 0.05$ .



**Fig. 8.** Ground cover (%) compared with months since last fire for five sites over 23 years. Linear regression lines fitted to data where  $P < 0.05$ .

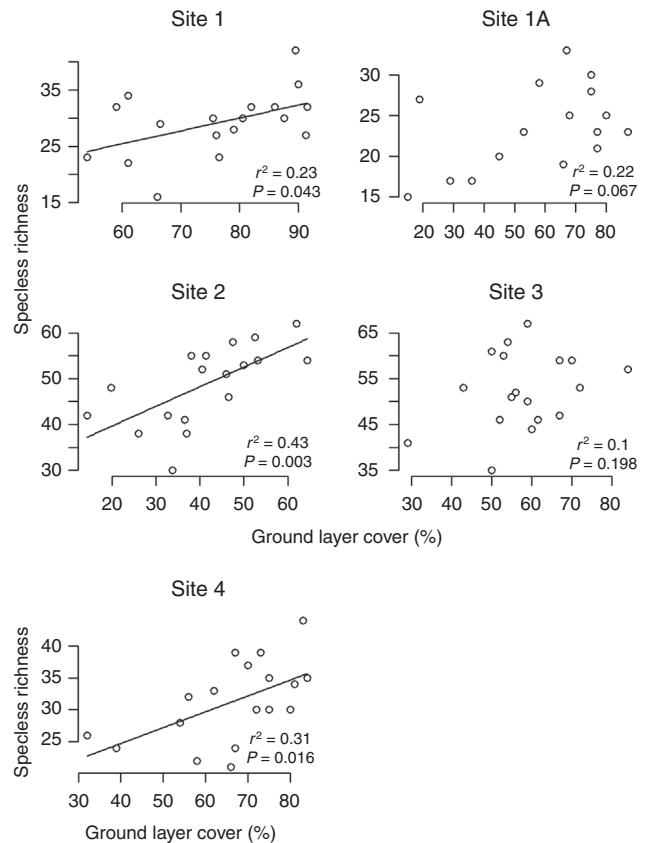
## Discussion

The dominant species composition and cover of the ground layer of these north-eastern Queensland tropical savanna communities remained remarkably similar over the 23 years of sampling. This was despite large variability in annual rainfall; i.e. 6 years with rainfall at least 250 mm below the long-term mean, and 4 years with rainfall greater than 400 mm above the mean. In addition, grazing pressure varied across the sites, and even though all sites were burnt across the 23 years, fires occurred at different frequencies, from 1 to 5 times per site.

The species richness of 23–53 species per 500-m<sup>2</sup> plot is similar to that of eucalypt savanna in the Northern Territory (Fensham 1990) and in Cape Cleveland north Queensland (Williams *et al.* 2003). The ground layer in this study is dominated by the perennial C<sub>4</sub> grass *T. triandra* and is similar to many savanna studies in the Northern Territory, although there is a frequent dominance of the biomass of annual grasses particularly *Sarga* spp. in the Northern Territory (Russell-Smith *et al.* 2003b; Andersen *et al.* 2005; Scott *et al.* 2012). The dominant ground layer in this study is more comparable to the 5-year study of Williams *et al.* (2003).

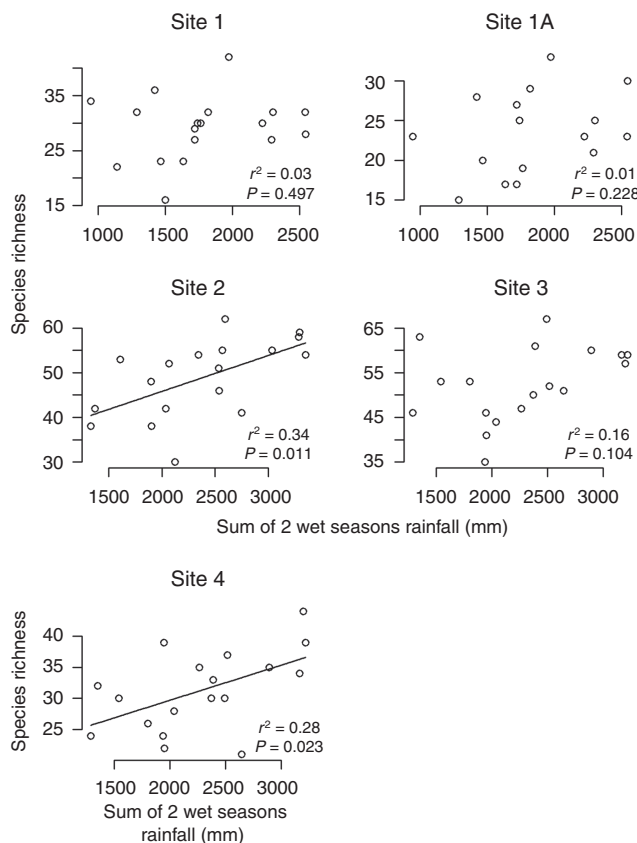
### Dominant species over time

The cumulative number of species recorded at a given site can only increase over time, because of events operating at three temporal scales; sampling effects, ecological changes such as succession and evolutionary changes (Preston 1960). Even



**Fig. 9.** Ground layer cover (%) compared with species richness for five sites over 23 years. Linear regression lines fitted to data where  $P < 0.05$ .

though some species may not be present at any particular sampling, e.g. subdominant perennial species with underground storage structures or annual species with low cover, the composition and cover of species recorded at each sampling allowed the sites to be consistently classified together (Fig. 4). Stability of ecological communities depends on species richness, species composition and the interactions between species (Ives *et al.* 2003), but also on disturbance, nutrient supply and climatic conditions (Bai *et al.* 2004). In this study, the dominant ground layer species, *T. triandra*, was always present at all sites and consistently had the highest cover (47–69% of the ground cover). *Themeda triandra* is one of the most widespread C<sub>4</sub> grasses in the world and is central to the ecological functioning of palaeotropical savannas (Snyman *et al.* 2013; Dunning *et al.* 2017). Other studies have shown that the ecological dominance of *T. triandra* is tied to periodic burning and can tolerate moderate grazing, relying on its ability to rapidly resprout after removal of biomass by fire or grazing (Morgan and Lunt 1999; Bond *et al.* 2003; Price *et al.* 2019). Tropical grasslands dominated by *T. triandra* and *Digitaria macroblephara* on the Serengeti Plains, central-east Africa, were also fairly stable with respect to plant composition over 7–10 years (Belsky 1985; Anderson 2008). The hypotheses that *T. triandra* is dependent on fire and grazing to persist in a savanna grassland (Danckwerts 1993; Snyman *et al.* 2013) is



**Fig. 10.** Species richness compared with the sum of the two previous wet season rainfall for five sites over 23 years. Linear regression lines fitted to data where  $P < 0.05$ .

inconsistent with Site 1, which over 28 years (23 of this study plus an observation in June 2020, M.R. Newton, pers. comm.) has maintained a *T. triandra* ground layer with only one fire and no cattle grazing in that period.

The perennial grasses *H. triticeus* and *Alloteropsis semialata* were also consistently present and subdominant in all sites across this study. The fire responses reported for *H. triticeus* are somewhat conflicting and may suggest an interaction between fire and grazing. *Heteropogon triticeus* is selectively grazed by cattle and it is common to see plants uprooted under even moderate grazing pressure (G. M. Crowley and S. T. Garnett, unpubl. data) in Crowley and Garnett (2001). In field experimental studies at Cape Cleveland, *H. triticeus* and *A. semialata* were significantly more abundant in plots burnt early in the dry season than in unburnt plots (Williams *et al.* 2003), whereas these species increased over time in both unburnt and annually burnt plots in north-central wetter savannas of the Northern Territory (Russell-Smith *et al.* 2003b). Scott *et al.* (2009) suggest that the dominant grasses *H. triticeus* and the annual *Sarga intrans* have declined in the Territory Wildlife Park because of the lack of fire and associated increase in mid-storey trees and litter cover, and these grass species require a fire at least each 7 years to ensure their persistence, and without fire over a 14-year period they are eliminated from a site.

### Core and occasional species

The finding that the ground layer of these savannas have stable dominant and sub-dominant species over time, and that there are a very large number of other species, supports the concept of assemblages being composed of core and occasional or satellite species. This has been proposed for other plant communities (Glenn and Collins 1990; Pärtel *et al.* 2001) as well as for fish (Magurran and Henderson 2003) and insects (Ulrich and Ollik 2004). The results of this study do not support the Carousel Model (van der Maarel and Sykes 1993) with the core perennial species (*T. triandra* and *H. triticeus*) maintaining their relative dominance over the 23 years of variable magnitude wet seasons and the disturbances of fires and grazing. Perennial subdominant grasses *Arundinella setosa* and *Eremochloa bimaculata* (Sites 2, 3 and 4), and *Mnesithea rottboellioides* (Site 4) were consistently present despite five fires and grazing over the 23-year period.

The distribution of species frequencies within sites was strongly bimodal (a peak for core species and another for satellite species) and shows some differences between lifeforms. In particular, a large proportion of graminoids had high frequencies, reflecting their dominance in cover. Anderson (2008) found that dominant grass composition in the Serengeti was also very stable through time, despite significant fluctuations in rainfall and in fires. Some of the occasional species in our study were very scarce, e.g. *Ischaemum rugosum* was initially observed in a drainage area adjacent to Sites 1 and 1A, known previously from a Herbarium specimen. Some distinctive vine species such as *Aristolochia holtzei* and *Ipomoea graminea*, which have subterranean tubers, have each been recorded on four occasions each (Site 1), but have not been recorded there since 2003 and 2007 respectively. The drivers for these changes in hidden diversity (Pärtel 2014) are unknown, although further long-term studies may offer the opportunity to better understand such changes over time. The exponents of species-time relationships in this study (ranging from 0.33 to 0.54) were comparable to mean values of 0.35–0.45 reported for grasslands from four North American studies detailed in White *et al.* (2006).

### Responses of non-native species

Only seven non-native species were widespread (recorded at every site) and a further eight were found only at a single site. The majority of non-native species had a cover of <1% on all occasions, suggesting they had played a limited role in the community structure of these savannas. This is in contrast to some areas of the wetter savannas of the Northern Territory where gamba grass (*Andropogon gayanus*) and other introduced African grass species have become dominant species and are altering fire regimes and vegetation structure and function (Rossiter-Rachor *et al.* 2009; Setterfield *et al.* 2010).

The impacts of invading species on native communities can range from no effects to large declines (Meffin *et al.* 2010). In our study, with sites subject to light grazing and irregular fire regimes, the native species are able to continue to dominate the

ground cover at these savanna sites, and resist invasive non-native species. Similarly, Day and Buckley (2013) found minor changes in species composition in New Zealand tussock grasslands over 25 years, despite the presence of three species of highly invasive *Hieracium* species, and concluded that the grasslands are stable. Although two recently introduced species to our sites, *Praxelis clematidea* and *Passiflora suberosa*, continue to increase in cover, to date the effects on species richness and ground cover are minimal. *Themeda triandra* has been found to be resistant to weed invasion in temperate areas (Prober and Lunt 2009). The introduced woody pasture legume *S. scabra* is present at all sites except Site 4 and increasing at Sites 1A and 3. *Stylosanthes scabra* is increasingly prevalent at the nearby (within 100 km) Brooklyn station after the removal of domestic stock 10 years ago (Kemp and Kutt 2020).

#### *Seasonal effects on the ground layer cover and richness*

The magnitude of the wet season rainfall was strongly correlated with the total cover of the ground layer, although it varied in strength across the sites. This correlation was most strong in the sites typically receiving less winter rainfall (Sites 1, 1A and 2). The tree canopy cover was generally sparse and varied little and was unlikely to be constraining the productivity of the ground layer. Canopy cover was not correlated with the ground layer cover or species richness. Whereas it might be expected that amount of rainfall in any particular wet season would affect the biomass and cover of the ground layer of a savanna, and therefore species richness. However, the direct relationship between rainfall and richness was inconsistent compared to those between rainfall and cover, or cover and richness (see Fig. 5, 9, 10). Similarly, in a study of a Californian annual grassland, Hobbs and Mooney (1995) found that relationships between individual species' abundances and rainfall were complex, with varying lags between rain and peak abundance contributing to hysteresis in community level variation in relative abundance.

#### *Fire effects on the ground layer*

There is a picture developing across northern Australia of stability in savanna ground layers with regular fires. This stability is based around a set of 'core species', especially perennial grasses, in regularly burnt sites. Savanna ground layers generally have a consistent post-fire flush of ephemeral species, with changes following longer intervals between fire (Williams *et al.* 2003; Scott *et al.* 2012; Lebbink *et al.* 2018). Disturbance theory is a key framework for understanding species coexistence in plant communities generally (Miller 1982) and in Australian temperate grasslands (Lunt and Morgan 2002; Price *et al.* 2019). The theory is that especially in highly productive environments, large dominant species, usually perennial grasses, monopolise resources such as light and outcompete and exclude most other species (Grime 1973; Grace 1999), as well regulating nutrient cycling and species population dynamics (Lunt 1997; Morgan and Lunt 1999).

In the tropical savannas where the seasons are generally predictable in their pattern and timing but variable in their

magnitude, the primary disturbance is fire, although in some cases it is grazing. Disturbance such as fire can increase species richness by removing the competitive dominance of perennial grasses (Price *et al.* 2019). This competitive exclusion is thought to be less strong in less productive situations, as rates of biomass accumulation are regulated by climate and soil fertility (Knapp and Smith 2001; O'Halloran *et al.* 2013; Harpole *et al.* 2016). The general hypothesis is that an intermediate level of disturbance will produce the highest species diversity (Miller 1982). Sites 2 and 3, which experienced five fires, and light grazing in Site 2, have the highest overall species diversity of the sites, which supports the hypothesis. Site 4 which also experienced five fires had lower species richness, as did the very infrequently burnt Site 1. The influence of site substrate is also a fundamental attribute in determining species richness (Scott *et al.* 2012; Lebbink *et al.* 2018). Site 1A, which experienced the highest level of disturbance mainly as grazing, had the lowest species richness and the highest non-native species contribution.

The situation in the tropical savannas is further complicated by the competition between the woody plants and the herbaceous community. The influence of fire on the woody plant-herbaceous plant balance has been the subject of multiple studies with the 'fire trap' hypothesis suggesting that regular fires inhibit woody tree recruitment (Bond *et al.* 2003, 2012), and the lack of fire leading to woody thickening and loss of ground layer species (Fensham 1990; Russell-Smith *et al.* 2003a; Williams and Centurino 2007). As found in other northern Australian studies, there is a complex relationship of bottom up environmental factors e.g. edaphic conditions and vegetation structure, and top down processes such as fire that interact to influence the ground layer composition (Scott *et al.* 2009; Williams *et al.* 2017).

In this study the species composition and cover of the dominant perennial grasses, primarily *T. triandra* and less dominant *H. triticeus* and other perennial grasses, is very stable over the 23-year study period and over the five sites. Four of these sites experienced 3–5 fires with intervals ranging from 1 to 10 years, whereas Site 1 experienced only 1 fire. This study documents stable savanna ground layers under regular burning (3–5-year intervals), however it does not show a decline in cover or species composition in the *T. triandra* dominated grassland that was only burnt once and not grazed in 23 years. Williams *et al.* (2003) found a significant decline in the dominant perennial *H. triticeus* without fire for 3 years at Cape Cleveland. In our study *H. triticeus* was consistently present at subdominant cover levels (2–10% of ground cover) in all sites across the 23 years, seemingly completely independent of the fire regime or lack of fire.

There were clear short-term effects of fire on the ground layer in this study, including appearance of ephemeral species in the samplings immediately after fires (Fig. S3), supporting the findings of Williams *et al.* (2003) who found that the abundance of several common species, including graminoids, ephemeral forbs and twining perennial forbs increased immediately after fire in north-eastern Australian savannas. However, there was no discernable longer-term effect of fires, or lack thereof, on the ground cover or species richness of the



ground layer in this study. Similarly, over a 5-year period in open savanna forest in Kaplaga in the Northern Territory (Andersen *et al.* 2005), there were no detectable effect of fire on floristic composition of the grass layer. The short-term increase in ephemeral species and perennial forbs after fire is usually attributed to the reduction in perennial grasses in semi-arid (Kutt and Woinarski 2007; Cowley *et al.* 2014; Fensham *et al.* 2015; Lebbink *et al.* 2018) and tropical vegetation (Williams *et al.* 2003; Andersen *et al.* 2005) in Queensland and the Northern Territory. The contribution of annual and ephemeral species in this study was low for all sites both in terms of cover and species richness. The effect of potentially more frequent and intense fires under more variable and extreme climate predicted for the region (Moise *et al.* 2015) will need to be studied, and continuing this long-term study will contribute to that research.

#### Grazing effects on the ground layer

Although grazing had visible effects on understorey biomass it had little effect on species composition or total ground cover in these savannas, comparing sites within the same rainfall areas. This is consistent with Fensham *et al.* (2005) who found that fire and grazing effects had insignificant long-term influences on both overstorey and understorey woody cover in semi-arid central Queensland forests. *Themeda triandra*, *H. triticeus* and *A. semialata* are considered to be palatable pasture species and are selectively grazed by cattle throughout the year (Crowley and Garnett 2001; Snyman *et al.* 2013; Dunning *et al.* 2017) but are consistently present in all the study sites indicating a low intensity grazing regime.

In this study, the paired Sites 1 (not grazed by cattle) and 1A (regularly grazed) offer an opportunity to examine the influence of fire and grazing quite directly, as the environmental conditions vary far less between the pair than they do between the other sites. Kemp and Kutt (2020) found the response after 10 years of removal of domestic stock from Brooklyn station, 15 km north of Sites 1 and 1A, varied with the land types, which included depositional (RE9.5.9b), metamorphic and granitic land zones. At Brooklyn there was as expected an increase in some palatable species and native herbaceous species overall, but also an increase in the number of non-native species, particularly the introduced pasture legume *S. scabra*. The paired sites (1 and 1A) had the lowest overall species richness (29.1 and 26.4) of the five sites. The grazed and more frequently burnt Site 1A had a lower ground cover, lower species richness and a higher contribution from non-native species. The lower and more variable ground cover is an expected result of grazing impact through the physical removal of biomass, and this disturbance also creates opportunities for establishment of non-native species. A high presence of non-native species and grazing may also reduce native species richness through competition and preferential grazing. However both of these sites had the lowest proportion of annual species (6.2% at 1) and interestingly the additional disturbances at Site 1A only raised the annual species richness to 6.4% of the total. So results here do not support a requirement for fire or disturbance to maintain *T. triandra* which still dominated Site 1 in June 2020.

#### The importance of site replication

Knowledge of temporal variability in community composition is undoubtedly useful in development of hypotheses relevant to theory, which might be tested through experiments. But it is also vitally important to be pragmatic regarding the important issue of sampling design for survey and assessment of savanna ecosystems, for example, by revealing the relative value of a single sampling in describing the ground layer community of tropical savannas (in terms of percentage floristic diversity capture). Approximately one-third of the species recorded at each site over the length of the study was recorded at the first survey. The timing of vegetation sampling in highly seasonal environments is also one of the critical factors in determining the proportion of the flora captured in a single sampling (Neldner *et al.* 2004). Observations of short-lived annual or short growing season perennial plants are generally the most affected by timing of sampling (Garrard *et al.* 2008), whereas perennial woody plants are generally detectable at any time of the year. For most survey and assessment activities, a sample site is visited only once, and this may not necessarily be in good seasonal conditions. In the long-term study reported here, sampling occurred at the end of the wet season, which has been shown to be the optimal time to obtain species presence and maximum ground cover (Neldner *et al.* 2004). Only 6–12% of the ground layer species found to occur at the site were recorded during every sampling event. Some plants have detection probabilities of less than one and can remain undetected at a site although present (Garrard *et al.* 2008) or may be in a life stage that is cryptic, e.g. terrestrial orchids (Kéry and Gregg 2003). For example, *Corybas barbarae* is a terrestrial orchid that has been observed above the surface on only five occasions over the 23 years of sampling at Site 4.

Nevertheless, for all sites (except Site 2 at 52%), more than 60% of the ground layer species observed in any given sample, were recorded in more than half of all samples of the site, and 100% of the dominant perennial grass species were recorded at every sampling. Still, there remains the need for several sites in the same vegetation type to be sampled, or the same site to be repeatedly sampled over time, to fully capture the diversity of a vegetation type. Conversely, if the ecological question is primarily about environmental gradients and sites are not spatially aggregated then a single survey may be adequate, as suggested by Schultz *et al.* (2014). Repeated site sampling is rarely practical for surveys, and often such assessments must be completed over short time periods, frequently less than 1 year, e.g. Environmental Impact Assessments. Thus, the requirement to replicate samplings spatially in the same vegetation type is generally accepted as necessary for comprehensive vegetation surveys, e.g. Neldner *et al.* (2020). Perhaps most importantly, not finding species in a single sampling event does not demonstrate that it will not occur there.

#### Conclusions

The ground layer of these north-eastern Queensland tropical savanna eucalypt communities appear to be very stable over decades, despite many species being infrequently recorded at any given site. The ground layers appear resilient to variations in yearly rainfall, and the effects of sporadic fires, light grazing

and the presence of non-native plants. The cover and composition of the herbaceous ground layer is consistently dominated by the core perennial grasses *T. triandra* and *H. triticeus*, with many species of facultative seeders (annuals – satellite species) collectively contributing minimally to the overall cover but significantly to richness. In total, 60% of the subdominant herbaceous plant were perennial and although not always apparent at the time of any particular sampling event, are assumed to have persisted as underground storage structures.

The rainfall variability year to year did not have a significant effect on ground layer cover or species richness. There were up to five fires and periods of light grazing by domestic stock at the sites, but these disturbances did not appear to have a significant effect on the ground layer total cover nor on number of species. The number of non-native plant species in the ground layer was low (<7% of species for three sites, and no more than 17% at the most disturbed site), with the stable native ground layer largely resisting invasion from adjacent disturbed areas. Repeat samplings over time, and additional samplings in space, are required to capture the full floristic variation that can occur within these communities.

### Conflicts of interest

The authors declare that they have no conflicts of interest.

### Declaration of funding

This research did not receive any specific funding. Queensland Herbarium management facilitated field work and provided staff resources to conduct the research.

### Acknowledgements

We thank Eda Addicott, Peter Bannink, John Clarkson, Wayne Harris, Mark Newton, Damian Milne, Ceri Pearce, John Thompson and Gary Wilson who assisted with the field data collection; Rosemary Niehus for preparing the map in Fig. S1. We also thank Rod Fensham, Gordon Guymer and anonymous reviewers for constructive comments on the paper.

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Handling editor: Dick Williams