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Mechanisms behind persistence of a fire-sensitive alternative stable state system in the Gibson Desert, Western Australia

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Abstract

Alternative vegetation types that switch from one to another under contrasting fire regimes are termed fire-mediated alternative stable states (FMASS). Typically, pyrophylic communities (i.e., vegetation assemblages favored by burning) dominate under high frequencies or intensities of fire. Conversely, fire-sensitive (pyrophobic) vegetation types persist under long fire-free conditions. As the persistence traits of plants of FMASS systems are generally poorly researched, threshold levels of pyric disturbance that trigger 'state-switching' are often unknown. Dense thickets of the obligate-seeder shrub waputi (*Aluta maisonneuvei* ssp. *maisonneuvei* [Myrtaceae]) form fire-retarding woody islands within highly flammable spinifex (*Triodia* spp.) grasslands in arid Australia. To examine the tolerance of *Aluta* thickets to burning, we investigated: (1) the influence of post-fire rainfall and fire severity on recruitment (a field study); (2) soil seedbank densities (a field study); and (3) fire-related dormancy cues in seeds (a germination trial). We found a positive relationship between recruitment and post-fire rainfall volume, and much higher mean recruitment at sites with high- (5.9 seedlings/m2) than low-severity-burnt (2.2 seedlings/m2) and unburnt shrubs (0.03 seedlings/m2). Post-fire regeneration was mediated by dense soil-borne seedbanks, and the germination trial indicated that smoke promoted germination. Although *Aluta* shrubs are invariably fire-killed, high-severity fires are unlikely to lead to state shifts from shrubland to grassland because of the ability of mature stands to regenerate from dense, fire-cued seedbanks. Nevertheless, given that *Aluta* seedlings are exceptionally slow-growing, post-fire droughts combined with fire-return intervals less than the *Aluta* primary juvenile period of c. 5 years could drive conversion from *Aluta*- to *Triodia*-dominated vegetation.

Keywords Arid zone · Alternative stable states · Ecotone · Fire ecology · Obligate seeder

Introduction

Alternative stable state theory holds that multiple ecosystem states can exist under the same environmental conditions (Peterson 1984; Sousa and Connell 1984). In flammable systems, alternative stable states may exist between fire-sensitive (pyrophobic) and fire-promoting (pyrophilic) vegetation, with clear boundaries and strongly differing

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structure and function usually segregating the two (Bond et al. 2005). Transitioning between alternative equilibrium states, or ‘state shifting’, typically occurs when some threshold level of fire frequency or intensity is reached (Pausas 2015; Pausas and Dantas 2017). Documented examples of fire-mediated alternative stable states (FMASS) include Patagonian forests and shrublands (Sottile et al. 2015), rain forests and moorlands in Tasmania (Jackson 1968; Wood and Bowman 2012), *Acacia* scrubs of the great dividing range of eastern Australia (Clayton-Greene and Wimbush 1988; Hunter 2005), and rainforests and grassy balds in the Bunya mountains of Queensland, Australia (Butler et al. 2014; Macdermott et al. 2017).

Most previous research of FMASS systems has focused on providing evidence to satisfy the criteria required to identify alternative stable states. These criteria include: (1) proposed alternative states can occupy the same environmental space; (2) alternative states are stable over more than one generation; (3) dominant species of alternative states may modify the environment to perpetuate their own existence; and (4) ‘state shifts’ occur when some threshold disturbance frequency or intensity is reached (Peterson 1984; Sousa and Connell 1984). Many proposed fire-sensitive alternative vegetation states have some tolerance to low-severity and/or infrequent pyric disturbance (Knox and Clarke 2012; Warman and Moles 2009). However, few studies have examined ecological mechanisms that enable fire-sensitive systems to persist under sub-threshold fire regimes. This represents an important research shortfall, as lack of such baseline ecological information makes predicting the response of fire-sensitive FMASS systems to variation in fire regime difficult. For conservation managers, this means uncertainty about what fire-management prescriptions will best conserve fire-sensitive vegetation states.

In this study, we examine mechanisms of post-fire persistence of fire-sensitive *Aluta maisonneuvei* (F.Muell.) Rye & Trudgen ssp. *maisonneuvei* (Myrtaceae) (common names desert myrtle and waputi) thickets in flammable *Triodia* spp. (Poaceae) (common name spinifex) grasslands in the Gibson Desert, Western Australia (Fig. 1a–d). Consistent with FMASS theory, *Aluta* thickets and *Triodia* grasslands occur on identical sandy substrates and each have contrasting tolerances to fire perturbation. Additionally, variations in fire regime are reported to trigger ‘state shifting’ between the two communities (Gill 2000; Wright 2018). Hence, from an international standpoint, they offer ideal study systems to examine mechanisms that drive transitions between FMASS systems.

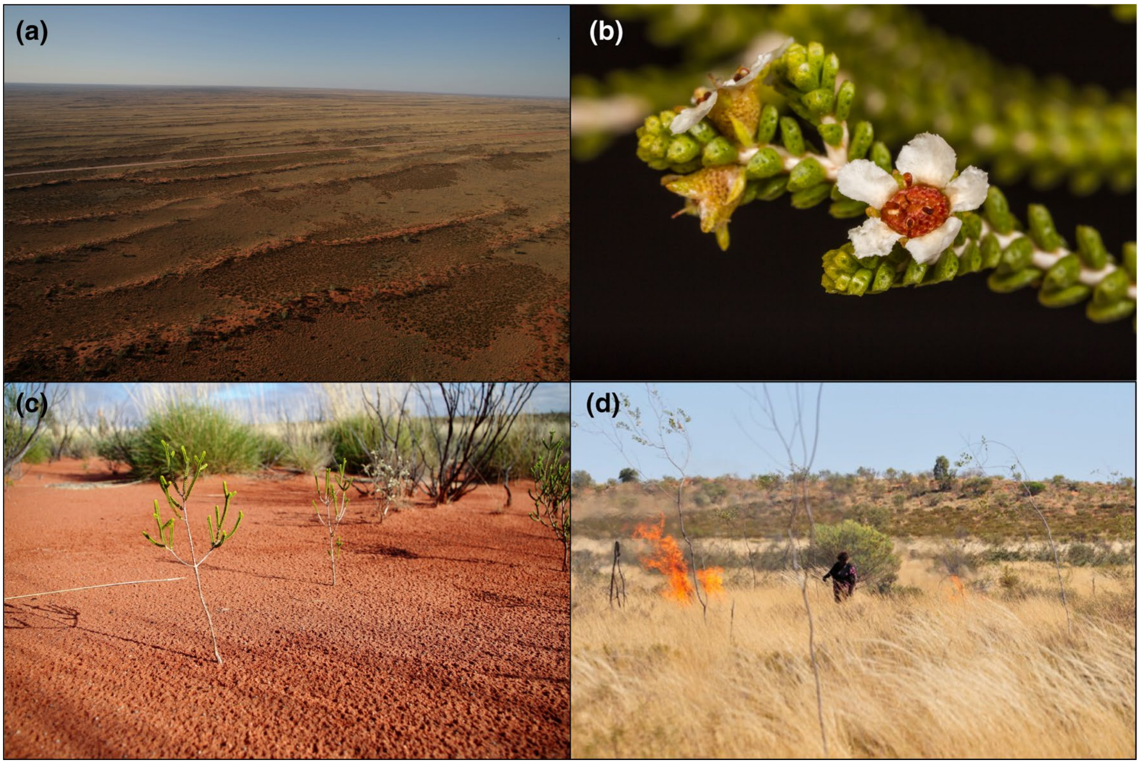

Fig. 1 Context of the Gibson Desert study system: **a** aerial view of *Aluta* thickets within parallel desert dunes dominated by *Triodia* grasslands; **b** *Aluta* flowers with prominent oil glands on leaves; **c** *Aluta* seedling recruitment after fire; **d** Pintubi management burning in *Triodia* grassland in the Kiwirrkurra Indigenous Protected Area, eastern Gibson Desert, Western Australia. Color version of this figure is available online

In the field, the pyrophilic nature of *Triodia* grasslands is obvious. *Triodia* grasslands promote fire by having well-aerated fuel architecture that burns easily, and many *Triodia* species also exude a flammable resin on their leaves (Buckley 1983, 1984). *Triodia* grasses are also somewhat tolerant of high-frequency fire cycles, being capable of reaching reproductive maturity within 3–36 months (depending on rainfall) and, therefore, able to return seed to the soil soon after initial post-fire establishment (Jacobs 1973; Armstrong 2011). In contrast, *Aluta* shrubs are fire-intolerant (i.e., they cannot resprout after fire), though the likelihood of fire carrying in the shrublands is reduced, because the understory is typically sparse or absent (i.e., the stands are often monospecific) (Duguid et al. 2008; Latz 2007). *Aluta* shrubs are also slow to reach reproductive maturity, with a primary juvenile period greater than 5-years (Wright 2018). Hence, they are favored by long fire-free intervals that allow seedbanks to replenish as stands age (Duguid et al. 2008; Latz 2007; Wright 2018).

Fire regimes in the Gibson Desert are typical of those in other parts of arid Australia. Grass growth and fuel accumulation is driven by cumulative rainfall, and large-scale wildfires typically occur after two or more successive years of above-average rainfall (Allan and Southgate 2002; Burrows et al. 2006). Mean fire-return intervals have been estimated at 8–30 years (Ward et al. 2014), though fire intervals shorter than 3 years can occur when exceptionally high post-fire rainfalls promote rapid post-fire fuel accumulation (Burrows et al. 2006). Under such circumstances, closely spaced 'follow-up' fires are generally not fueled by *Triodia* grasses, but by fast-growing short-lived grasses, particularly *Aristida holathera* Domin. (Griffin et al. 1983). Fire severity in *Triodia* grasslands in the Gibson Desert is typically high due to high fuel loads and hot weather conditions during the summer months when most fires burn (Burrows et al. 2006). Fire severity in *Aluta* shrublands is also usually high, as high wind conditions that increase burn intensity are usually required to allow flames to spread from shrub-to-shrub above the sparse or non-existent understory.

The current study examined the post-fire regeneration capacity of mature *Aluta* stands within *Triodia* grasslands in the Gibson Desert. Initially, a mensurative field study was conducted to quantify seedling recruitment rates in response to variation in fire severity and post-fire rainfall volume. Then, to further investigate the capacity of stands to regenerate from seedlings after fire, we: (1) assessed seedbank densities and the vertical distribution of seeds in seedbanks in the field; and (2) conducted a germination trial using fresh and aged seeds to investigate whether seeds have dormancy broken by the fire-related cues of heat and smoke. In concert, these studies provided insight into whether FMASS *Aluta* thickets are resilient to individual long-interval fire events, or are fire-intolerant and in need of active management to prevent fire incursions from surrounding *Triodia* grasslands.

Methods

Study site and species

All study sites were in the western portion of the Kiwirrkurra Indigenous Protected Area (KIPA), along the Port Headland Rd between Kiwirrkurra community and Nyinmi outstation. The KIPA is located within the Gibson Desert, which comprises a variety of land systems, including large areas of lateritic gibber plains, occasional low lateritic ridges, and extensive areas of undulating sand plain and dunefield. All sites of the current study were in dunefield systems. The climate of the KIPA corresponds to the "grassland hot (persistently dry)" climate-type of the Köppen classification, and the 20-year mean annual rainfall from the nearest reliable weather station (Walungurru [Kintore] airport c. 40 km east of the eastern KIPA boundary) is 296.1 mm (Australian Government Bureau of Meteorology 2019). Dunefield soils in the desert are typically red, deep siliceous sands that are highly infertile and possess little development of organic layers. Overstorey vegetation of the hummock grasslands within the dunefields is usually comprised of a sparse shrub layer dominated by one or more species of *Acacia* Mill., *Corymbia* K.D.Hill & L.A.S. Johnson, *Eremophila* R.Br., *Grevillea* Knight, *Hakea* Schrad. & J.C.Wendl., or *Senna* Mill.

The study taxon, *Aluta maisonneuvei* subsp. *maisonneuvei*, is a widespread shrub that exists in many Australian arid zone conservation reserves and provides important habitat for rare fauna such as the northern and southern marsupial mole (Bennison et al. 2013; Green 1980; Griffin 1984; Rye and Trudgen 2000). It is believed to be primarily outbreeding, owing to the presence of protandrous flowers and nectaries that facilitate pollination by small insects (Rye and Trudgen 2000). The seeds are enclosed within an indehiscent woody fruit, and the papery sepals are retained for sometime following dispersal, presumably promoting wider dispersal by wind or water (Rye and Trudgen 2000). *Aluta* flowering mainly occurs between April and October and estimates of flower production in a single year range from c. 8000 to 120,000 flowers/shrub (Online Resource 1). Despite such prolific flowering, seed set percentages are usually extremely low (e.g. < 1–2%) (Green 1980; Rye and Trudgen 2000). However, the causes of these high rates of flower abortion are not known and have not been investigated.

Relationships between fire severity, post-fire rainfall, and recruitment

The relationship between fire severity, post-fire rainfall, and seedling recruitment was examined at seven field sites via a mensurative field experiment conducted over three field trips in June and October 2016 and September 2017. These sites were of differing time-since-fire (TSF), ranging from 2 to 6 years TSF at the time of sampling (Online Resource 2). At each site, 10 high-severity-burnt, 10 low-severity-burnt, and 10 unburnt shrubs were randomly selected using the stratified random sampling approach of Harding (2012). Burn severity classes were assigned to individual *Aluta* skeletons based on the 'mean minimum diameter of burned branch' index (MMDB) of Moreno and Oechal (1991). Assignment to the 'high-severity' burn class required the mean diameter of 10 randomly selected burnt twigs of an *Aluta* skeleton at 1 m height to be ≥ 3 mm. Conversely, assignment to the 'low-severity' class required the mean diameter of 10 randomly selected burnt twigs at 1 m height to be ≤ 1 mm. Seedling numbers were counted beneath each shrub within a circular zone with radius 1 m directly beneath the shrub canopy, with the shrub's trunk as the centroid. The fire histories (i.e., time-since-fire) of each site were obtained from the North Australia and Rangelands Fire Information website (2019). The 6-, 12-, and 18-month post-fire rainfalls of each site were estimated using rainfall data from the nearest rainfall station at Walungurru Aboriginal settlement (Kintore) (Australian Government Bureau of Meteorology 2019).

Germination biology

The germination biology of *Aluta* was investigated via a germination trial with a four-factor orthogonal experimental design. The treatments examined were: (1) heat-stimulation, with the levels: control [unheated], 80 °C for 5 min, and 100 °C for 5 min, (2) smoke water application, with the levels: 'smoked', with the fruits (hereafter termed seeds) soaked in smoke water (dilution 1:10) for 24 h prior to the commencement of the trial, and 'not smoked', (3) incubation temperature, with the levels: 'winter' with temperatures set at 5 °C overnight and 20 °C during the daytime [simulating wintertime temperatures at 0–1 cm depth in dunefield soils (Wright and Fensham 2016)], and 'summer' with temperatures set at 20 °C overnight and 35 °C during the daytime [simulating summertime temperatures at 0–1 cm depth in dunefield soils (Wright and Fensham 2016)]; and (4) seed age, with the levels: 'fresh', with seed collected from the soil surface and to 0.5 cm deep, and 'aged', with seed collected from 1–2 cm depth.

Given the low estimated viability of the seed samples being used for the trial (1.5–2% viable, sample $n = 3 \times 200$), five replicates of 1000 seeds were used for each of the 24 treatment combinations. This allowed for an estimated c. 15–20 viable seeds per replicate. Following treatment, seeds were kept moist with rainwater and incubated for 45 days in cabinets in clear 18 cm-diameter plastic petri dishes on agar (dilution rate of agar in de-ionized water was 1:100). Prior to the agar study, an initial germination trial was conducted using blue card germination pads. However, germination on the cards was minimal, with only one germinated seed out of c. 100,000 seeds at the end of 4 weeks. The decision to use agar as an alternative germination medium was based on similar findings of agar-promoted germination for certain species of *Juncus* (Cyperaceae) and *Phyla canescens* (Verbenaceae) (Whalley, W. pers. comm. 2018). The improved germination response observed following incubation in agar is believed to have occurred, because, in many cases, germination conditions using agar more closely correspond to field conditions where some proportion of individual seeds are exposed to air (Whalley, R.D.B. pers. comm. 2018). When using germination pads, a meniscus frequently forms over seeds, which can completely deprive seeds of exposure to air.

Counts of germinated *Aluta* seeds in agar were recorded weekly for the duration of the experiment. Germination was defined as the emergence of the radicle from the seed. At the end of the experiment, a tally of the number of viable but un-germinated seeds per tray was made by sectioning all seeds and examining for healthy endosperm.

Seed populations in the soil

The vertical distribution of seeds in the soil was assessed by sampling soil cores beneath ten randomly selected unburnt shrubs at two sites in September 2017. A pilot study revealed that minimal seeds were present in soil layers below 4 cm. Consequently, only the uppermost 0–4 cm soil layer was sampled. Beneath each shrub, a single randomly positioned 40 × 40 cm column of soil to 4 cm depth was excavated, and the following three layers were carefully extracted using a paint scraper and a steel ruler: 0–1 cm, 1–2 cm, and 2–4 cm. In the lab, seeds were extracted and counted out from the samples following the flotation method of Price et al. (2010). In this procedure, each sample was immersed in 100 ml of potassium carbonate solution (500 g L^{-1} water) and then agitated for 30 s and left for 5 min to allow the organic matter to suspend in the solution. The samples were then rinsed thoroughly under running water and left to dry overnight in an oven at 80 °C. The following day, seeds were counted out and crushed and a dissection microscope was then used to estimate percentage seed viability at each site and within each soil layer by assessing the proportion of fruits with a developed seed (i.e., with white-colored fleshy tissue) from a sub-sample ($n = 1000$). An estimate of the number of viable seeds at each soil layer was then made by multiplying estimated proportional seed viability at each soil depth by the total seed count. Where less than 1000 seeds were present in a sample, the entire sample was examined for viable seeds under a dissection microscope.

Statistical analysis

All data sets were initially explored following the protocol of Zuur et al. (2010), and model validation for all analyses followed the protocol of Zuur and Ieno (2016). All analyses were carried out in R version 3.5.2 (R Core Team 2018). For the analysis of the recruitment data set, a generalized linear mixed modeling (GLMM) framework was used with ‘site’ employed as a random intercept to account for dependencies due to observing multiple shrubs at each site. For this analysis, relationships between seedling counts and the categorical variable ‘fire severity’ and the continuous covariate ‘18-month rainfall’ were tested using a negative binomial generalized linear mixed model (NB GLMM) in the package ‘glmmTMB’ (Brooks et al. 2017). TSF was initially considered for inclusion in the model for this analysis. However, during data exploration, variance inflation factors (VIF) indicated collinearity between 18-month rainfall and TSF (VIF = 3.19). Examination of the data set indicated that this was because by chance the most recently burnt sites had experienced very high post-fire rainfall totals; whereas sites with longest time-since-fire were subjected to post-fire drought (i.e., TSF and post-fire rainfall were negatively correlated). Retaining collinear variables in GLMM analyses inflates standard errors of parameter estimates (Zuur et al. 2010). Consequently, given that post-fire rainfall has been reported as a strong determinant of post-fire seedling survival in many Australian systems (Keith 1996; Croft et al. 2010), only the 18-month post-fire rainfall covariate was retained. The inability to include TSF in this analysis means that caution should be exercised in interpreting the results, as it is possible that some factor associated with increasing TSF (e.g., density-dependent seedling mortality and seedling growth rate) could also have affected post-fire seedling numbers at the sites. Post hoc comparisons with Bonferroni corrections were conducted using the ‘emmeans’ package (Lenth 2019) to assess the significance of differences in seedling counts between the various levels of fire severity.

For the germination analysis, we used a binomial generalized linear model in the ‘lme4’ package (Bates et al. 2015). The response variable in this analysis was the number of germinated seeds per sample tray out of the total number of viable seeds in each tray. This analysis tested the effects of ‘seed age’, ‘heat’, ‘smoke’, and ‘incubation temperature’ on the proportion of seeds that germinated. As in the recruitment analysis, post hoc comparisons with Bonferroni corrections were conducted to assess the significance of differences in germinant counts between the various levels of the treatments.

To assess whether total seedbank density differed between soil depths and/or between sites, an NB GLMM was conducted in the ‘glmmTMB’ package. For this analysis, a generalized mixed modeling framework was used with ‘shrub identity’ employed as a random intercept to account for dependencies due to observing seeds from different depths from the same soil core at each shrub. To assess whether viable seedbank density differed between soil depths and/or between sites, a Poisson GLMM was conducted in the ‘lme4’ package. As in the other analyses, post hoc comparisons with Bonferroni corrections were conducted to assess the significance of differences in seed counts between the various soil depths.

Results

Post-fire rainfall and fire severity both strongly affected post-fire *Aluta* recruitment. Increasing fire severity was associated with increasing levels of recruitment, with more than double the mean recruitment at high-severity-burnt shrubs (5.9 seedlings/m^2 [SE = 0.7)) than low-severity-burnt shrubs (2.2 seedlings/m^2 [SE = 0.4]), and almost no recruitment at unburnt shrubs (0.03 seedlings/m^2 [SE = 0.01]) (Table 1, Fig. 2). In addition, there was a strong positive relationship between 18-month post-fire rainfall and seedling number. The lowest levels of recruitment were observed at Eastern 2 site (0.6 seedlings/shrub, Online Resource 2, Fig. 2)], and this site experienced the lowest levels of post-fire rainfall among the sites [32.6 mm in 18 months from April 2007 to September 2008 (Australian Government Bureau of Meteorology 2019)]. Increasing levels of recruitment were observed at sites that received increasing levels of post-fire rainfall (Online Resource 2, Fig. 2).

The germination analysis indicated no effect of heat treatment on seed germination. However, it did detect a significant three-way interaction between the smoke, incubation temperature, and seed age treatments (Table 1). This three-way interaction indicated that the relationship between smoke treatment and seed germination differed at different incubation temperatures, but that the direction of this two-way relationship depended on seed age. This complex interplay of effects is illustrated in Fig. 3, where it can be seen that smoke treatment improved germination at both summer and winter incubation temperatures for ‘aged’ seeds (left panel, Fig. 3), but had no effect on germination of ‘fresh’ seeds incubated at winter incubation temperatures and only a marginally significant effect on germination of ‘fresh’ seeds incubated at summer temperatures (right panel, Fig. 3).

The analysis of the depth distribution of total seed counts (‘viable’ plus ‘non-viable’) in the seedbank indicated no differences in total seed counts between sites (Table 1). However, there was a significant soil depth effect

Table 1 Estimated regression parameters, standard errors, *z* values, and *P* values for germination, recruitment, and seedbank (SB) GLM and GLMM analyses

Study/experiment	Parameter	Estimate	Standard error	*z* value	Pr (> |*z*|)
Germination trial	Intercept	0.91	0.14	6.68	< 0.0001
	Smoke yes	0.89	0.23	3.86	0.00011
	Age fresh	− 2.21	0.21	− 10.30	< 0.0001
	Incubator winter	− 3.63	0.30	− 12.12	< 0.0001
	Smoke yes: age fresh	− 0.18	0.32	− 0.56	ns
	Smoke yes: incubator winter	2.19	0.37	5.84	< 0.0001
	Age fresh: incubator winter	1.32	0.54	2.46	0.0139
	Smoke yes: age fresh: incubator winter	− 1.83	0.66	− 2.78	0.0054
Recruitment study	Intercept	2.63	0.19	13.85	< 0.0001
	Rainfall 18-month post-fire	0.66	0.18	3.64	0.0002
	Fire severity low	− 0.96	0.15	− 6.56	< 0.0001
	Fire severity unburnt	− 3.69	0.37	− 9.94	< 0.0001
Seedbank study (total seeds)	Intercept	6.92	0.57	12.10	< 0.0001
	Site Nyinmi	0.81	0.80	1.02	ns
	Depth 1–2 cm	− 1.06	0.20	− 5.27	< 0.0001
	Depth 2–4 cm	− 2.12	0.21	− 9.91	< 0.0001
Seedbank study (viable seeds)	Intercept	2.12	0.41	5.14	< 0.0001
	Depth 1–2 cm	− 0.76	0.10	− 7.75	< 0.0001
	Depth 2–4 cm	− 2.41	0.19	− 12.63	< 0.0001

Germination trial tested effects of smoke, incubation temperature (summer vs. winter temperatures) and seed age on germination response. Recruitment study tested effects of fire severity and post-fire rainfall on seedling numbers. SB study tested effect of site and soil depth on seed counts

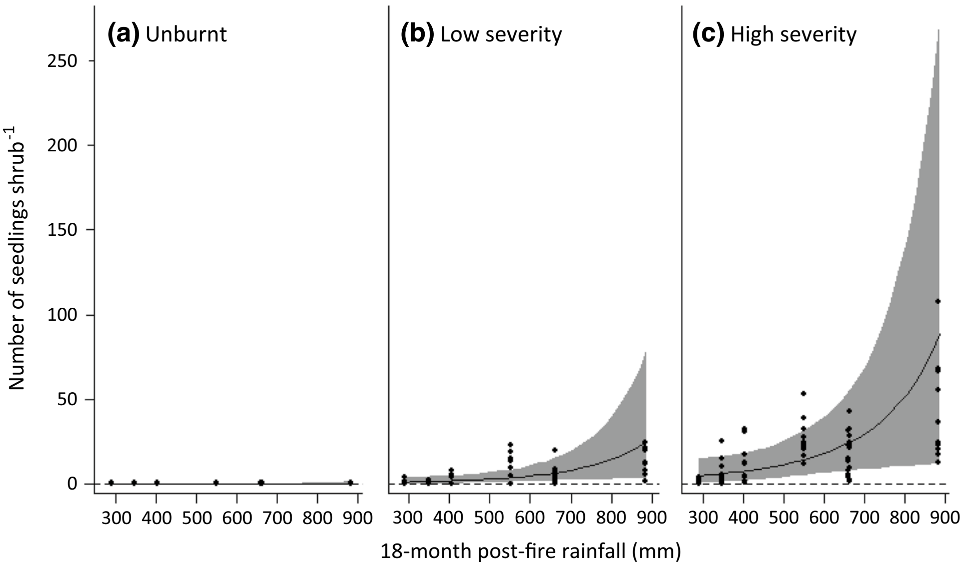

Fig. 2 Relationship between the expected number of seedlings shrub^{-1} and 18-month post-fire rainfall for **a** unburned, **b** low fire severity, and **c** high fire severity. Shaded areas indicate 95% confidence bands around the fitted values from the GLMM analysis

(Table 1), with more than double the amount of seeds at the 0–1 cm depth (18075.5 seeds/m^2, SE = 5672.3) compared to the 1–2 cm depth (7495 seeds/m^2, SE = 2737.4), and more than 12 times the number of viable seeds at the 0–1 cm depth than the 2–4 cm soil depth (1405.2 seeds/m^2, SE = 402.9) (Fig. 4, left panel). The analysis of viable seed counts also detected a significant soil depth effect (Table 1), with more than double the mean number of viable seeds at the 0–1 cm [127.1 seeds/m^2 (SE = 49.8)] than the 1–2 cm [60.4 seeds/m^2 (SE = 33.4)] depth, and more than 12 times the number of viable seeds than the 2–4 cm depth [10.6 seeds/m^2 (SE = 5.1)] (Fig. 4, right panel).

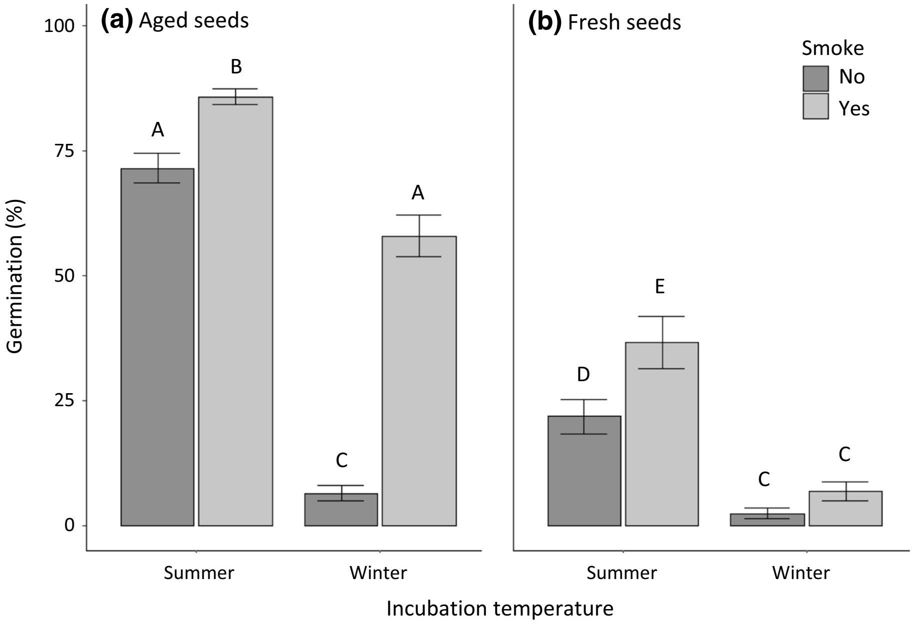

Fig. 3 Relationship between mean *Aluta* seed germination (%) (± SE) and smoke treatment, seed age (see opposing facets—aged vs. fresh), and incubation temperatures (summer vs. winter). Bars with different letters are significantly different at $P < 0.05$ according to GLM post hoc testing

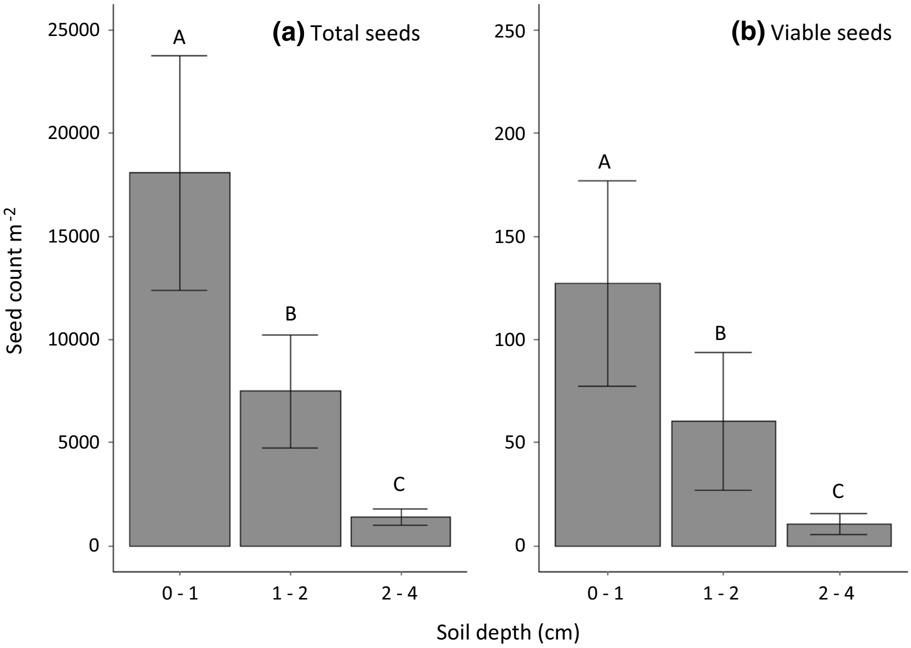

Fig. 4 **a** Total (viable plus non-viable) and **b** viable Aluta seed counts m^{-2} sampled at three levels of soil depth. Bars are means (± SE); bars with different letters (within panels) indicate means differ at $P < 0.05$ according to GLMM post hoc testing

Discussion

Aluta thickets are typical of many fire-sensitive FMASS systems in that their persistence is promoted by long fire-free periods, and the likelihood of burning is reduced in mature communities because fuel loads are minimal in the understorey (AWC 2016; Duguid et al. 2008; Gill 2000). In addition, as the current study showed, *Aluta* shrubs have strong capacity to regenerate from seedlings after individual fires with sufficient post-fire rainfall, with most sites in the KIPA showing strong recruitment after both high- and low-severity burning. This combination of community and species properties that confer fire resistance suggests that considerable inertia to ‘state shifting’ exists in *Aluta* and *Triodia* systems. If this is the case, major changes in community assemblages due to fire may be rare in these communities, and active management to conserve *Aluta* shrublands may not be necessary under prevailing climatic norms.

Despite this apparent resistance to ‘state change’, there are two situations that could contribute to equilibrium shifts between *Aluta* and *Triodia* vegetation. First, our recruitment analysis indicated that severe post-fire drought can reduce the capacity for *Aluta* populations to recover after fire, presumably by eliminating post-fire seedling cohorts. Consistent with this, droughts have been shown to significantly alter competitive and recruitment outcomes after fire in several systems (Keith 1996; Marond et al. 2004; Van Nieuwstadt and Sheil 2005; Croft et al. 2010). Nonetheless, protracted post-fire dry periods of the 'intensity' experienced by sites such as the drought-affected 'Eastern 2' site in our study are not common in the Gibson Desert. This site received only c. 30 mm of rainfall during an 18-month period shortly after burning (Online Resource 2), and the rainfall records of the Walungurru weather station indicate that this was the driest 18-month period, since weather recording began at this station in 2001. Moreover, at the Giles Weather station c. 300 km to the south of the study area, there has only been one instance in 61 years of weather monitoring that annual rainfall has gone below 50 mm. Consequently, although severe post-fire drought does appear to strongly impede seedling survival in *Aluta* stands after fire, it may not be a common phenomenon in the Gibson Desert study region.

The second situation that could contribute to equilibrium shifts between *Aluta* and *Triodia* vegetation is short fire intervals. As *Aluta* juveniles are slow-growing and take > 5 years to reach reproductive maturity, fires occurring at intervals less than 5 years could lead to the elimination of seedling cohorts and to the exhaustion of the viable seedbank. If these two factors operated in tandem (i.e., a severe post-fire drought was succeeded by a fire interval of < 5 years), assemblages dominated by *Triodia* grasses would presumably be favored. This is because *Triodia* are strongly xerophytic, having several leaf adaptations that reduce transpiration and enable them to tolerate long dry periods (Grigg et al. 2008; Jacobs 1973; Wells 1999), and they also have a shorter primary juvenile period comparative to *Aluta* (Jacobs 1973, 1984, Wright 2018).

The resilience to pyric perturbation evident in *Aluta* communities appears to be related to several factors. First, having dense and persistent soil-borne seedbanks means that propagule sources are always available for population regeneration, irrespective of whether the perturbation is a severe drought or fire. The maintenance of these persistent seedbanks may be facilitated by: (1) high rates of annual flowering that ensure regular input to seedbanks; (2) high quantities of essential oils in the seeds (Brophy et al. 2000), which may deter seed predators; (3) extremely low levels of seed viability which may reduce predation by making viable seeds more difficult for predators to locate (Traveset 1993; Ramos-ordonez et al. 2008); and (4) physiological dormancy, which ensures staggered germination over time and allows seedbanks to accumulate until optimal conditions for germination occur (Ooi 2007). Another factor likely to promote resilience to pyric perturbation is the burial of a considerable proportion of seedbanks at depths > 10 mm. Seeds buried at or below this depth would be likely to escape lethal heating during burning, as previous studies indicate that low-fuel load *Triodia* fires do not heat soils beyond 60 °C at 10 mm depth (Bradstock et al. 1992; Wright and Clarke 2008), and heating to 100 °C in our germination trial had no negative effect on *Aluta* seed germinability.

Given that a large proportion of seeds germinate even without smoke, (c. 25% across all treatment groups from our germination trial), it is unclear why *Aluta* recruitment is almost absent in unburnt thickets. It is possible that in unburnt stands, seedling survival is constrained by strong root competition from adult shrubs. Germination without smoke could, therefore, be a bet-hedging strategy for an unpredictable climate and fire-return period, allowing for germination in very long unburnt stands where adults simply die of old age (Nevoux et al. 2010; Müller et al. 2013). Inhibition of recruitment in unburnt vegetation could also be caused by secondary metabolites in soils, which are leached from litter/leaves/roots as stands age (i.e., allelopathy). In support of this hypothesis, leaf material and litter from closely related Thryptomene species and other genera in the Myrtaceae are high in volatile compounds such as sesquiterpenes and phenolic, cinnamic, and benzoic acids (Dastlik et al. 1989; Uddin et al. 2014). These compounds have been shown to suppress seed germination and inhibit plant processes such as hormonal balance, respiration, and photosynthesis (Dastlik et al. 1989). In addition, some of these compounds are known to be readily volatilized by heat, so high soil temperatures during fire may provide a mechanism that removes these compounds from soils (White 1986). The 'allelopathy' hypothesis may, therefore, account for observed increases in recruitment after high-severity compared to low-severity burning. High-severity fires, which are usually accompanied by higher soil temperatures than low-severity fires, should have increased capacity to destroy soil-borne allelopathic compounds that might otherwise impede recruitment.

Croft et al. (2010) argued that the combined effects of fire and drought should be taken into consideration in fire-management practices. In the Gibson Desert, the effects of fire and drought on FMASS communities may become a highly relevant issue in the future, due to anthropogenic climate change (ACC). Under ACC, temperatures are expected to increase and rainfall patterns will become progressively more unpredictable (Parmesan and Hanley 2015). These climatic changes will exacerbate heat stress, evaporation and instability within local arid zone climates. Such instability in climate and increases in the severity of drought and possibly fire may favor the expansion of *Triodia* grasslands into *Aluta* shrublands. Active management in these systems may, therefore, have to be more adaptive to counter unidirectional shifts towards more fire-promoting vegetation.

Conclusions

Aluta shrubs are fire-sensitive at the shrub-level but fire-tolerant at the population-level, with razed stands capable of mass seedling regeneration after a single fire. If fire incursion from *Triodia* grasslands occurs, recruitment is mediated by dense seedbanks that are triggered to germinate by smoke and are buried at sufficient depths to avoid lethal heat during fire. A situation that could trigger state shifting for *Aluta* populations is if stands are burnt at intervals less than the primary juvenile period (i.e., < c. 5 years) and/or have insufficient rainfall following fire to permit establishment (i.e., considerably lower rainfall than average during the 18-months post-fire). In such circumstances, it would be improbable for the dormant seedbank to be maintained and declines in populations could occur. Given this, contemporary burning practices of the Pintupi Aboriginal peoples in the KIPA appear likely to promote the persistence of *Aluta* thickets. By regularly burning surrounding *Triodia* grasslands under cool, low-wind conditions, the likelihood of fire incursions into the shrublands should be reduced. This, in turn, should increase the probability that fire intervals will be sufficiently spaced to allow shrubs to reach reproductive maturity and replenish seedbank densities after fire. Nevertheless, with higher temperatures and climatic instability predicted under future ACC scenarios, these fire-management methods may need to be increasingly adaptive and take into consideration post-fire drought effects on *Aluta* recruitment.

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Data accessibility Data available from the TERN AEKOS Digital Repository.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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