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Does resilience to fire confer resilience to grazing in savanna ant communities of Northern Australia?

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Abstract

Introduction Evolutionary traits acquired in response to one type of disturbance will potentially confer resilience to other disturbances that have similar environmental impacts, even if the biota has no evolutionary history of such disturbances. In grassy ecosystems the environmental impacts of grazing have important similarities to those of fire through the removal of grass biomass, and we hypothesise that high resilience to frequent fire confers high resilience to grazing.

Aims We test this hypothesis by investigating the resilience of highly fire-resilient ant communities to grazing in a mesic Australian savanna, which has not historically experienced such high levels of mammalian grazing.

Methods We sampled ants using pitfall traps at Annaburroo Station in the Australian seasonal tropics using ten plot triplets, with each triplet representing no, low and heavy grazing. Grazing has had a major impact on the basal area of perennial grasses and the cover of bare ground. We considered large (>4 mm) ants only, which tend to be particularly sensitive to disturbance.

Results We recorded 28 species of 'large' ants from 14 genera. Neither ant species richness nor overall composition varied significantly with grazing, and only one of the eight most common species responded to grazing.

Discussion Ant communities at Annaburoo Station are highly resilient to livestock grazing. The limited number of relevant studies suggest that ant communities in Australian savannas more generally have higher resilience than those in southern rangelands where fire frequency is relatively low. This supports our hypothesis that an evolutionary history of frequent fire confers resilience to grazing. Many more studies are required, but we suggest that resilience to grazing might be related more to evolutionary history in relation to fire, a more pervasive remover of plant biomass globally, than to grazing.

Implications for insect conservation Grazing by cattle is the dominant land-use in Australian savannas and the Australian savanna ant fauna is one of the richest on Earth; our findings of high resilience is therefore good news for insect conservation. Such good news is likely to have wide applicability to other fire-prone grassy ecosystems subject to livestock grazing.

Keywords Biodiversity conservation · Ecological memory · Grazing impacts · Rangeland management · Tropical savanna

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Introduction

The resilience of biological communities - their ability to return to their prior state after disturbance - is fundamental to their ecological dynamics (Holling 1973). Resilience is strongly influenced by 'ecological memory', defined as the ability of past states or experiences to affect the contemporary response of a community to disturbance (Thompson et al. 2001; Bengtsson et al. 2003; Johnstone et al. 2016). This means that different ecosystems with different ecological memories are likely to support biological communities that differ in their resilience (Moretti et al. 2006; Moretti and Legg 2009; Laliberte et al. 2010; Peco et al. 2012).

Ecological disturbance plays a fundamental role in the dynamics of most ecosystems (Sousa 1984). Survival and regeneration strategies in relation to disturbance are responses to disturbance impact rather than to the agent of disturbance itself (Keeley et al. 2011). This implies that evolutionary traits acquired in response to one type of disturbance can confer resilience in relation to other disturbances that have similar environmental impacts, despite having no direct experience with these other disturbances (Peterson 2002; Keeley et al. 2011). For example, fire removes vegetation biomass, especially from the ground layer, and, more than fire itself, this provides the evolutionary pressure for plant and animal responses (Whelan 1995; Bond and Van Wilgen 1996). It means that adaptive traits in relation to fire should also be effective for other agents of disturbance that similarly remove plant biomass and therefore create similar environmental conditions.

In addition to fire, grazing is another major agent of disturbance in grassy ecosystems worldwide (Bond and Parr 2010) that similarly acts to remove plant biomass from the ground layer (Crawley 1983; Ash et al. 1997; Ash and Corfield 1998; Laycock 1991). Fire is obviously different from grazing in that it has little selectivity and can result in the complete removal of above-ground grass biomass. Fire also consumes grass biomass in a single pulse rather than being an ongoing pressure (Archibald and Hempson 2016). However, the effects of fire persist until grass biomass is restored, which is typically at least several months. Given that fire frequency is often very high, even annual, in grassy ecosystems (Parr et al. 2014), this means that the effects of grass consumption by fire can occur for a substantial proportion of overall time. Moreover, frequent fire results in persistent reductions in litter cover in grassy ecosystems, both through direct consumption (Cook 2012) and by reducing woody cover (Sankaran 2005). Both fire and grazing therefore act to increase openness of the ground habitat, which is a critical factor mediating faunal responses to disturbance (Andersen 2019). It can thus be hypothesized that communities with an evolutionary history of frequent

fire will also have high resilience to heavy grazing, even if they have had no direct experience of it. This has important implications for biodiversity conservation given that livestock grazing is a dominant land-use in grassy ecosystems throughout the world.

With most areas burning every 2–3 years (Andersen et al. 2003; Russell-Smith et al. 1997; Russell-Smith and Yates 2007), Australian savannas are among the world's most fire-prone biomes, and, as in other savannas, have experienced frequent fire throughout their evolutionary history (Bourlière1983; Hutley and Setterfield 2019). Consequently, the Australian savanna biota is highly resilient to frequent fire (Williams et al. 2003; Andersen et al. 2005; Andersen 2021;). The dominant land-use across Australian savannas is grazing by cattle (Australian Bureau of Agricultural and Resource Economics and Sciences 2016). It is likely that current grazing pressure by mammalian herbivores is now higher than it has ever been, given that the native megaherbivores that were driven to extinction following the arrival of humans about 50,000 years ago tended to be browsers rather than grazers (Johnson 2006), and the abundance of extant native herbivores is generally low due to low-nutrient soils, water limitation and predation (Eldridge et al. 2016; Letnic et al. 2009). We hypothesise that despite no evolutionary history of high grazing pressure, faunal groups showing high resilience to frequent fire are also highly resilient to high levels of grazing.

Here we test this hypothesis by investigating the resilience of ant communities to grazing in a mesic Australian savanna. Such ant communities show especially high resilience to frequent fire (Andersen et al. 2012, 2014) because they are dominated by arid-adapted taxa that are favoured by the open habitats that are maintained by high fire frequency (Andersen 2003, 2007; Andersen and Vasconcelos 2022). We therefore predict that these communities will also be highly resilient to grazing, more so than ant communities without an evolutionary history of frequent fire. Previous studies in Australian savannas at Lakefield Station (1,050 mm mean annual rainfall; Arcoverde et al. 2017) and the Victoria River District (< 650 mm; Hoffmann 2000) in the Northern Territory showed ants to be highly resilient to grazing, but the extent to which such resilience extends to more mesic savannas remains unknown. Disturbance might be expected to have greater impacts in areas of higher rainfall because of higher vegetation complexity (Andersen 2019). In this paper we examine ant responses to grazing in the far north of the Northern Territory, where mean annual rainfall exceeds 1,500 mm.

A global review of ant responses to livestock grazing found that the foraging abundances of typically between 25 and 50% of ant species that could be analysed statistically were significantly affected (Hoffmann 2010). We specifically
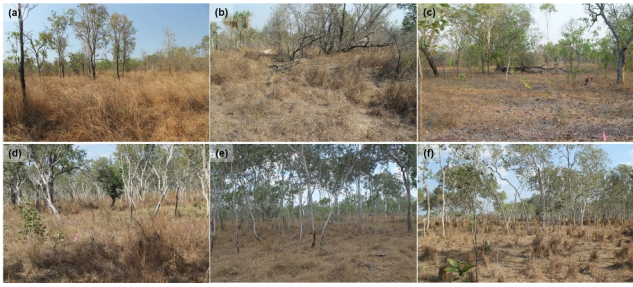
Fig. 1 Photos of study sites from two triplets on Annaburroo Station, Northern Territory, Australia, showing effects of grazing (a, d – no grazing; b, e – low grazing; c, f – high grazing) on ground-layer vegetation

predict that this figure will be markedly less than 25% in our study. We first examine the effects of grazing on the structure of ground-layer vegetation, to document the extent to which grazing affects key habitat variables for ants. We then describe the effects of grazing on ant communities, using a simplified assessment protocol that considers larger species (>4 mm) only. The targeting of larger ant species for assessment of disturbance impacts has proven to be highly efficient and reliable, providing similar results to those of entire ant communities (Andersen et al. 2002; Arcoverde et al. 2018). Moreover, larger ant species tend to be especially sensitive to disturbance (Gibb et al. 2018; Ness et al. 2004), and so if anything we would expect to find greater impacts of grazing than is the case for entire ant communities.

Materials and methods

Study area

The study was conducted at Annaburroo Station, a 308 km² cattle station located 100 km southeast of Darwin in Australia's Northern Territory. The area experiences a tropical monsoonal climate, with its mean annual rainfall of 1522 mm heavily concentrated in a summer wet season from December to April (Bureau of Meteorology 2022). Mean temperature shows relatively little variation between summer (mean maximum and minimum temperatures of 36.4 ℃ and 25.5 ℃ respectively) and winter (31.7 ℃ and 19.2 ℃). The vegetation is savanna woodland dominated by evergreen species of *Eucalyptus* and *Corymbia*, with an understory dominated by C4 perennial grasses (Egan and Williams 1996).

Annaburroo is an ideal location for the study of grazing impacts because it includes an extensive conservation corridor connecting two national parks, where grazing has been excluded for >20 years. Our study design was based on cross-fence comparisons inside and outside the conservation corridor (Fig. 1). The corridor runs east-west and then

north-south for about 10 km with a width of approximately 100 m, and cattle are managed differently in the paddocks on either side. For at least the past five years cattle have been held throughout the year to the south and east, but for only six months on the other side; we refer to these areas as experiencing high and low levels of grazing respectively. It was therefore possible to locate plots of no, low and high levels of grazing in very close proximity to each other, and we established ten such triplets of plots (Fig. 1) spread along the conservation corridor, with triplets separated from each other by at least 100 m.

Sampling

Ants were sampled in each of the 30 plots using 20 pitfall traps (45 mm-diameter plastic specimen containers, partly filled with ethylene glycol as a preservative), arranged in a line with 10 m spacing between traps. 'No' transects were located along the centre of the conservation corridor, and 'Low' and 'High' transects were located approximately 30 m from the corridor fences and thus approximately 80 m from 'No' transects. Traps were operated for a 48-hr period in September 2014.

Larger ants were sorted and identified following Andersen et al. (2002) using a body length guideline of >4 mm. We specifically defined large ants as all species within the genera *Lioponera*, *Rhytidoponera*, *Anochetus*, *Odontomachus*, *Leptogenys*, *Platythyrea*, *Pseudoneoponera*, *Camponotus*, *Oecophylla*, *Polyrhachis* and *Opisthopis*, as well as species of the *rufoniger* and *curtus* groups of *Melophorus*, the *rothsteini* group of *Monomorium*, and the *purpureus* group of *Iridomyrmex* (see Andersen 2000 for these groups). Ants were sorted to species, and when possible named, following the species nomenclature of Shattuck (2000). Species that could not be named were identified to species group following Andersen (2000) and assigned code numbers (sp. 1, etc.) following those of previous studies in the Top End of the Northern Territory (Andersen et al. 2016). Voucher specimens of all species are deposited in the ant collection held at the CSIRO Laboratory in Darwin. Species abundances were recorded and capped at 100 per trap to avoid data distortions caused by a very large number of individuals from a single colony falling into one or a few traps (see Andersen 1991).

We measured ground-layer structural variables likely to be affected by grazing using 1 m × 1 m quadrats centred on each pitfall trap location (n = 20 per plot) to visually estimate the percentage basal area of perennial grasses, and the percentage cover of herbs (annual grasses and forbs), litter, and bare ground.
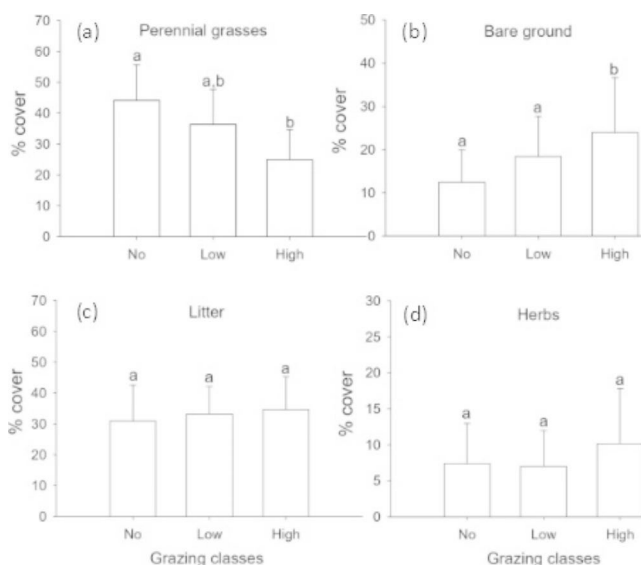
Fig. 2 Mean (±SE) percentage of cover of (a) perennial grasses, (b) bare ground, (c) litter and (d) herbs in relation to three grazing classes on Annaburroo Station, Northern Territory, Australia

Analysis

We used linear regression models to analyze the relationship between grazing level and ground-layer habitat variables. Herb cover was highly correlated ($R > 0.7$) with the cover of perennial grasses, and so we excluded it from analysis. Linear regressions were checked for outliers, overly influential observations, homoscedasticity and normal distribution of residuals. Analyses were performed using the *multcomp* package in R (R Core Team 2014).

We used GLMs to analyze variation in ant abundance and species richness in relation to grazing level and environmental variables. We used Poisson error distribution for species richness and Quasi-Poisson error distribution for abundance to account for over-dispersed data (Crawley 2012). We also conducted GLMs on the individual abundances of the most common species, defined as those occurring at >9 sites and

with >50 total individuals. For GLMs with grazing level (a categorical variable), we established "no grazing" as the basis for comparisons with other grazing levels. Models were checked for outliers, overly influential observations, homoscedasticity and normal distribution of residuals. Analyses were performed using the *car* and *multcomp* package in R (R Core Team 2014).

We used Canonical Correspondence Analyses (CCA) to evaluate variation among sites in ant species composition (based on species abundance data), and how such variation was associated with grazing level and ground-layer habitat variables (Ter Braak 1986; Legendre et al. 2011). We conducted randomization tests (10,000 randomizations) to check the statistical significance of grazing level and habitat variables (Legendre et al. 2011). The CCA and randomisation analyses were performed using the *vegan* package in R (R Core Team 2014).

Results

Ground-layer habitat variables

The basal area of perennial grasses (Fig. 2a) decreased with increasing grazing level, from nearly 50% under no grazing to about 25% under high grazing, and the cover of bare ground (Fig. 2b) increased from about 10–25% under no and high grazing respectively (Table 1). The cover of neither litter (Fig. 2c) nor herbs (Fig. 2d) varied in relation to grazing (Table 1).

The ant fauna

We recorded a total of 13,158 'large' ants from 28 species and 14 genera (Supplementary material Appendix 1, Table A1). The richest genera were *Rhytidoponera* (6 species) and *Camponotus*, *Leptogenys*, *Opisthopsis*, and *Polyrhachis* (each with 3 species). The most common species were

Table 1 Summary results after model averaging the effects of grazing intensity on environmental variables in Annaburroo Station, Northern Territory, Australia. No grazing was chosen as a base level to compare the other grazing intensities. Estimate = model averaged regression coefficient; SE = unconditional standard error, CI = 95% confidence intervals for regression coefficient estimates. *P < 0.05

| Response variable	Parameter	Estimate	p-value	Lower CI	Upper CI
Perennial grasses	Intercept	44.15	<0.001*	37.11	51.19
	Grazing low	-7.8	0.12	-17.76	2.16
	Grazing high	-19.2	<0.001*	-29.16	-9.24
Bare ground	Intercept	12.45	<0.001*	5.9	19.0
	Grazing low	5.92	0.2	-3.34	15.19
	Grazing high	11.5	0.017*	2.23	20.77
Herbs	Intercept	7.39	<0.001*	3.39	11.39
	Grazing low	-0.39	0.88	-6.05	5.27
	Grazing high	2.78	0.32	-2.87	8.44
Litter	Intercept	30.89	<0.001*	24	37.7
	Grazing low	2.38	0.61	-7.22	12
	Grazing high	3.81	0.42	-5.79	13.41
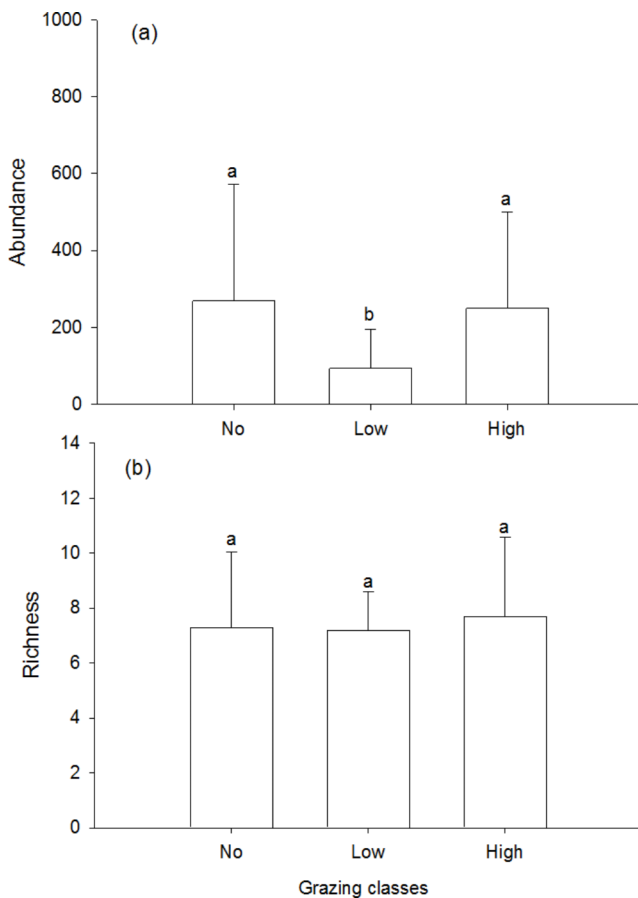
Fig. 3 Mean (± SE) total ant abundance (a) and species richness (b) in relation to three grazing classes on Annaburroo Station, Northern Territory, Australia

Iridomyrmex sanguineus (representing 65% of all ants, recorded from 86% of the plots), *I. reburrus* (12%, 25%) and *Monomorium maryannae* (9%, 301%); these three species together represented 86.% of all 'large' ants recorded.

Responses to grazing

Total ant abundance was significantly lower in the low grazing treatment than in the other treatments, which did not vary significantly from each other (Fig. 3a; Table 2). Mean ant richness showed no variation in relation to either grazing (Fig. 3b; Table 2) or to the ground-layer habitat variables influenced by grazing. However, it increased with increasing litter cover (Table 2).

Eight species were common enough for statistical analysis, and the abundance of only one (12.5%) of these varied significantly with grazing level: the abundance of *Iridomyrmex sanguineus* in low-grazing plots was half or less than in no and high plots (Fig. 4; Table 2). The overall abundance of the harvester ant *Monomorium maryannae* was far higher in the absence of grazing (Table S1), but nearly

all records were from just two plots and so the differences are not statistically significant. The abundances of two of the other common species varied with habitat variables that were influenced by grazing, but they did not vary with grazing; the abundance of *Melophorus* sp. 59 increased with the increase of bare ground, and the abundance of *Iridomyrmex reburrus* decreased with increasing cover of perennial grasses (Table 2).

Overall species composition did not vary with grazing ($\chi^2 = 0.089$, F = 1.109, DF = 1, p = 0.308; Fig. 5) or with any ground-layer habitat variables.

Discussion

Our study tested the hypothesis that the high resilience of ant communities to fire in Australian savannas confers high resilience to livestock grazing, because fire and grazing have many similar effects on ant habitat structure, and adaptive responses to disturbance relate to disturbance impact rather than to the agent of disturbance itself. We found strong effects of grazing on ground-layer habitat structure, substantially reducing grass basal area and increasing the cover of bare ground. Reductions in the cover of perennial grasses and increases in the cover of bare ground are typical effects of even low levels of livestock grazing globally, due to the combined effects of removal of grass biomass and trampling (Ash et al. 1997; Eldridge et al. 2011; Tongway and Ludwig 2011).

The cover of perennial grasses and bare ground are often particularly important variables influencing the structure of savanna ant communities (Parr et al. 2004; Vasconcelos et al. 2008), but, despite this, the marked effect of grazing on them in our study was not translated to major impact on ant communities. The abundance of only one species common enough for statistical analysis, *Iridomyrmex sanguineus*, varied significantly among grazing levels. Its abundance was lowest under low grazing and this was a driver of the same pattern in overall ant abundance. *Iridomyrmex sanguineus* is an ecologically dominant ant throughout monsoonal Australia and has a strong preference for open environments (Andersen 2000). It is heavily favoured by frequent fire (Andersen et al. 2012) and its abundance was promoted by grazing at Lakefield Station elsewhere in the Northern Territory (Arcoverde et al. 2016). We are unable to explain its pattern of abundance in relation to grazing in our study.

Only 12.5% of common species in our study showed a detectable response to grazing, which is markedly less than the 25–50% typically reported globally (Hoffmann 2010). We acknowledge that only eight of our 28 sampled species were common enough for statistical analysis and that the

Table 2 Summary results after model averaging the effects of each variable on total abundance and abundance of most common ant species and functional groups in Annaburroo Station, Northern Territory, Australia. No grazing level was chosen as a base level to compare the other grazing intensities. Estimate = model averaged regression coefficient; SE = unconditional standard error, CI = 95% confidence intervals for regression coefficient estimates. * P < 0.05

| Response variable	Parameter	Estimate	p-value	Lower CI	Upper CI
Abundance	Intercept	5.59	< 0.001*	5.03	6.27
	Grazing low	-1.05	0.017*	-1.94	-0.17
	Grazing high	-0.07	0.87	-0.96	0.80
Richness	Intercept	1.56	< 0.001*	1.11	2.0
	Litter	0.01	0.038	0.0005	0.025
Iridomyrmex sanguineus	Intercept	-6.11	< 0.001*	4.45	7.45
	Grazing low	-1.47	0.04*	-2.95	-0.22
	Grazing high	-0.85	0.21	-2.18	0.45
	Perennial grasses	-0.03	0.07	-0.07	0.002
	Bare ground	0.021	0.31	-0.02	0.06
Iridomyrmex reburrus	Intercept	4.48	< 0.001*	2.48	6.17
	Perennial grasses	-0.06	0.04*	-0.12	-0.005
Melophorus sp.59	Intercept	-9.95	0.003*	-16.86	-4.84
	Grazing low	0.8	0.224	-0.48	2.11
	Grazing high	2.01	0.057	0.18	4.18
	Bare ground	0.14	< 0.001*	0.08	0.23
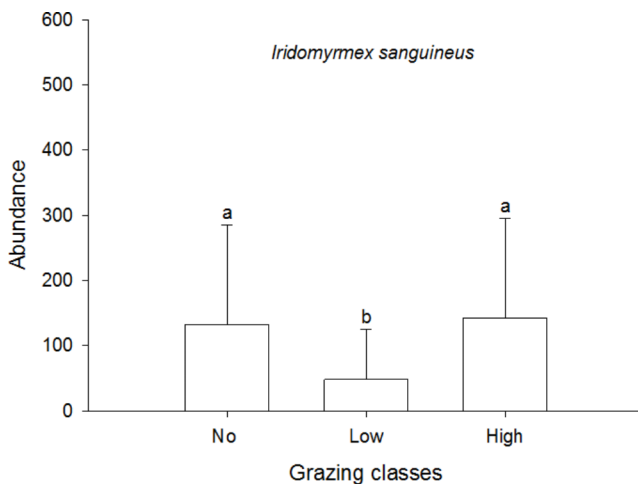
Fig. 4 Mean (± SE) abundance of *Iridomyrmex sanguineus* in relation to three grazing classes on Annaburroo Station, Northern Territory, Australia

Fig. 5 Canonical Correspondence Analysis of ant species composition at the 36 study plots on Annaburroo Station, Northern Territory, Australia. Variation in species composition was not related to either grazing or ground-layer habitat variables (p = 0.308)

responses of these common species may not reflect those of rare species. We also acknowledge that with additional sampling we may have obtained data on a larger number of species. However, we note that neither species richness nor composition varied with grazing, and these both considered all 28 of our sampled species. Moreover, our sampling intensity was comparable to that of other studies showing far higher responsiveness among common species. For example, in a South Australian rangeland where sites were similarly surveyed by a single bout of 20 pitfall traps, 34% of common species were found to be affected by grazing (Hoffmann and James 2011).
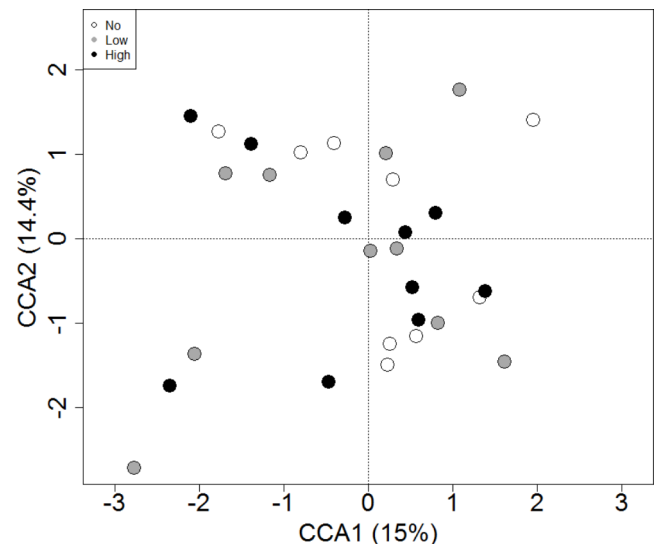
At Lakefield Station (1046 mm mean annual rainfall) elsewhere in the Northern Territory only three (10%) out of the 30 ant species common enough for statistical analysis responded to grazing, and grazing had no significant effect on either species richness or composition (Arcoverde et al. 2017). The proportion of common species affected by grazing in the Victoria River District southwest of Lakefield was also very low (17%, out of 12 species analysed; Hoffmann 2000). Our findings at Annaburroo Station indicate that similar resilience occurs in mesic savannas. Combining results from the three studies, the abundances of only six (12%)

out of the 50 species analysed were significantly affected by grazing. It therefore seems clear that ant communities in Australian savannas are particularly resilient to grazing when compared with the global average (25–50% of common species significantly affected; Hoffmann 2010).

The figure of 16% of common species significantly affected by grazing across the three savanna studies in the Northern Territory is far lower than the average of 36% from three relevant studies in central and southern Australia (Arcoverde et al. 2018; Hoffmann and James 2011; Landsberg et al. 1997), where fire is far less frequent, occurring at intervals from one to many decades (Edwards et al. 2008; Nano et al. 2012). The number of studies is too low for formal statistical analysis, but the results are consistent with the notion that ant communities of Australian savannas, where fire frequency is extremely high, are more resilient to grazing than are those from other Australian rangelands, where fire frequency is relatively low. Whatever the case, the high resilience of Australia's savanna ant fauna to grazing is good news for biodiversity conservation given that this fauna likely contains several thousand species and is possibly the richest in the world (Andersen and Vasconcelos 2022).

High fire frequency is a feature of tropical savannas worldwide (Bourlière 1983). If high resilience to fire also confers high resilience to grazing in savannas regardless of their evolutionary experience with grazing, then this has important implications for international comparisons of grazing impacts in savannas. For example, it would be predicted that ant communities in African savannas that support high biomasses of native mammalian herbivores would not necessarily be more resilient to grazing than are ant communities in other savannas. The effect of grazing on ant communities in African savannas remains almost totally unknown (see Mauda et al. 2017) and so data are not available to test this prediction. There have been a number of studies of the effects of pastoralism on ant communities in Brazilian savannas (Pacheco and Vasconcelos 2012; Pacheco et al. 2013, 2017), and these studies indicate a high degree of resilience. However, livestock grazing in Brazilian savannas is typically on introduced pastures following land clearing, and so the data are not directly comparable quantitatively.

In conclusion, our findings of exceptionally high resilience of ant communities to grazing in Australian savannas are consistent with the hypothesis that high resilience to frequent fire confers high resilience to grazing. Many more studies are required, but we suggest that resilience to grazing globally might be related more to evolutionary history in relation to fire, a more pervasive remover of plant biomass, than to grazing.

Table S.1

Ant species list, showing total abundances at sites with different grazing intensities (No, Low and High) at Annaburroo Station, Northern Territory, Australia

Species	Grazing class		
	No	Low	High
DORYLINAE			
Lioponera sp.4 (*singularis* gp)	0	0	1
ECTATOMMINAE			
Rhytidoponera sp.9 (*tenuis* gp)	7	14	27
Rhytidoponera borealis	11	6	6
Rhytidoponera aurata	0	0	1
Rhytidoponera brunnea	10	0	0
PONERINAE			
Anochetus paripungens	1	1	7
Odontomachus nr.*turneri*	14	30	24
Leptogenys exigua	6	32	1
Leptogenys nr.*conigera*	1	0	0
Leptogenys adlerzi	1	0	0
Platythyrea parva	0	5	0
Bothroponera sp.4 (*sublaevis* gp)	2	0	0
MYRMICINAE			
Monomorium maryannae	270	6	11
DOLICHODERINAE			
Iridomyrmex reburrus	0	81	141
Iridomyrmex sanguineus	1325	481	1425
FORMICINAE			
Melophorus sp.5 (*curtus* gp.)	35	56	28
Melophorus sp.59 (*curtus*)	70	59	123
Melophorus sp.1 (*rufoniger* gp)	7	4	14
Oecophylla smaragdina	8	16	4
Opisthopsis haddoni	10	6	10
Opisthopsis sp.1 (*haddoni* gp)	13	13	6
Opisthopsis rufonigra	5	2	2
Camponotus 'crozieri'	3	10	13
Camponotus 'novaehollandiae'	1	1	3
Camponotus sp.9 (*novaehollandiae* gp)	9	13	8
Polyrhachis senilis	12	3	7
Polyrhachis sp.12 (*obtusa* gp)	0	3	1
Polyrhachis sp.9 (*obtusa* gp)	1	0	0

Declarations

Authorship The study was conceived and designed by Gabriela Arc-

overde and Alan Andersen. Data collection and analysis were performed by Gabriela Arcoverde, who also wrote the first draft of the manuscript. All authors commented on previous versions of the manuscript and read and approved the final manuscript.

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