Rare plant species do not occupy water-remote refuges in arid environments subject to livestock grazing

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Abstract. In many of the world's arid regions there has been a dramatic increase in grazing pressure with herds of livestock sustained by the provision of artificial water points. In these systems it has been suggested that grazing-sensitive plant species will have contracted to refuges distant from water points where grazing impacts are low. This association was tested using a large data set of presence/absence records for rare plant species throughout the northeastern Australian arid zone. The presence records of only one of 45 species were statistically associated with lower grazing activity, as a function of distance-to-water, than the absence records. The field observation that this species is rarely grazed suggests it is not susceptible to grazing pressure. In general, the study supports assertions that populations of short-lived plants in drylands are resilient in the face of exaggerated livestock grazing because herbivores are not in sufficient densities to have an impact during the sporadic periods of high rainfall when plants can complete their life cycles. However, long-lived palatable species may be extinction-prone in grazed landscapes over long time frames if recruitment is curtailed by grazing.

Key words: Australia; livestock grazing; plant life forms; rare plants; semiarid; water-remote habitat.

Introduction

It has been suggested that the effects of commercial livestock grazing on ecosystem structure, function and composition may be most severe in arid environments (Eldridge et al. 2016). The consequences of these effects for biodiversity may be substantial given the ubiquity of livestock grazing as a land use throughout the world's drylands. An alternative view recognizes climate as the primary driver of vegetation dynamics in dryland rangelands with "boom-and-bust" climates, with grazing having a relatively minor effect. Proponents of this "non-equilibrium" theory recognize that the forage under variable climates is only abundant for brief sporadic periods amid frequent protracted drought, keeping livestock numbers well below the level where they can affect the vegetation community (Ellis and Swift 1988, von Wehrden et al. 2012, Engler and von Wehrden 2018). The analysis of long-term grazing exclosures has generally supported the resilience of community composition in the face of livestock grazing in Australian semiarid rangelands (Silcock and Fensham 2013). However, the same authors and others recognize that palatable

plant species can be removed in dryland grazing systems (Landsberg et al. 2003, Seymour et al. 2010, Silcock and Fensham 2013) particularly in continents with a low evolutionary exposure to grazing (Cingolani et al. 2005).

Modern rangeland pastoralism in arid areas is highly dependent on a network of artificial water points, such as ground-water bores or large dams. The resulting increased herbivore grazing pressure restricts grazing-sensitive plant species to water-remote habitat areas, which are the only remaining areas resembling pre-pastoral conditions (James et al. 1999, Landsberg et al. 2002, 2003). The notion of a relatively grazing-sensitive arid-zone flora is most relevant to locations such as the Australian continent. Here there is a sharp divide between pre- and post-pastoralism in the former, there were low densities of large native herbivores and in the latter high densities of managed herds of livestock, a proliferation of exotic herbivores, including rabbits (Scanlan et al. 2006) and goats (Pople and Froese 2012), and enhanced densities of native herbivores (Silcock et al. 2013). Water-remote gradients have been considered relevant to the vegetation of drylands in North America (Hart et al. 1993, Fusco et al. 1995), but in Africa, where large wild herbivores have persisted and there are ancient traditions of subsistence rangeland herding (Freier et al. 2014) the possibility of a grazing-sensitive flora persisting in water-remote locations is less tenable.

Even in Australia, however, it has proved difficult to identify grazing-sensitive species associated with water-remote refuges (Fensham and Fairfax 2008). This is largely due to the limited statistical power associated with infrequently recorded species. When a species is apparently restricted to water-remote sites, but is only found at a handful of locations in a patchy environment, it is possible that it occurred there by chance rather than due to grazing sensitivity (Fensham and Fairfax 2008). The major study, which presents quantified data to support the theory of grazing "decreasers" (Landsberg et al. 2003) employs an analysis based on relatively few sampling stations across a broad range of environments. In a more habitat-specific study from a recently grazed arid ecosystem, only one species out of 35 was restricted to areas of extremely low grazing pressure and it was so infrequently recorded that it could have occurred there by chance (Fensham et al. 2010).

Although grazing by domestic livestock is frequently cited as a cause of decline for threatened plant species in Australian rangelands (Leigh and Briggs 1992, Woinarski and Fisher 2003), the adaptation of many species to the "boom and bust" climatic conditions (Morton et al. 2011) may confer some resistance to grazing. For example, many species have an ephemeral life form, growing rapidly and setting seed during rain events and preserving seed in the soil during long drought periods (Sullivan and Rohde 2002). Some perennial species have adaptations that deter grazing, such as chemical compounds rendering plants toxic or unpalatable (Rebollo et al. 2002) or mechanical defenses such as tough foliage or sharp spines at least when plants are young (Burns 2014). However, long-lived shrubs may be susceptible to grazing if seed production and recruitment is inhibited by browsing (Auld 1993, Silcock et al. 2014).

Despite the limited evidence for grazing-sensitive species associated with water-remote refuges, the conclusion of Landsberg et al. (2003) that more species increase in abundance with distance to water than decline suggests that further examination of these patterns is required (Fensham and Fairfax 2008). Previous studies have expended effort generating complete species lists from stratified samples at various distances from water points (Fusco et al. 1995, Landsberg et al. 2002, 2003, Fensham et al. 2010). This may identify species that are still common in the landscape but exhibit a decreasing trend in relation to grazing, but does not efficiently generate data on species that may have become rare because of grazing. We apply an alternative approach by considering the species known to be rare in drylands of Australia (Silcock et al. 2011) and assessing their association with distance to water as a proxy for grazing relief. We hypothesize that some of these species are rare because of their grazing sensitivity and will be more likely to occur at sites further from water points where grazing activity is low. We also predict that this spatial bias will be more pronounced for perennial plants than ephemeral species, and for palatable species compared to

unpalatable species. The implications of the results for theories of resilience and flora conservation in drylands in the face of livestock grazing are discussed.

METHODS

Study area

The study area encompasses about 700,000 km^2 (Fig. 1), and comprises the northeastern section of the Australian drylands where mean annual rainfall decreases on a southwesterly gradient from 500 mm along the eastern and northeastern boundary to 130 mm in the southwest (Fig. 1), but is highly variable both within and between years. Summer temperatures are hot with maxima through December–February averaging 35–38°C and regularly exceeding 40°C, while short winters are characterized by cold nights (5–10°C), often falling below zero in the southern half of the area, and warm days averaging 20–27°C (Jeffrey et al. 2001).

Higher rainfall areas in the east support *Acacia* and, to a lesser extent, *Eucalyptus* woodlands, while the more arid portions are dominated by stony plains, grasslands, floodplains, low-relief sandstone ranges, open shrublands dominated by *Acacia* species, and extensive linear dune fields.

Between the extinction of the Pleistocene megafauna around 45,000 yr ago and the advent of pastoralism 150 yr ago, inland Australia has probably supported low
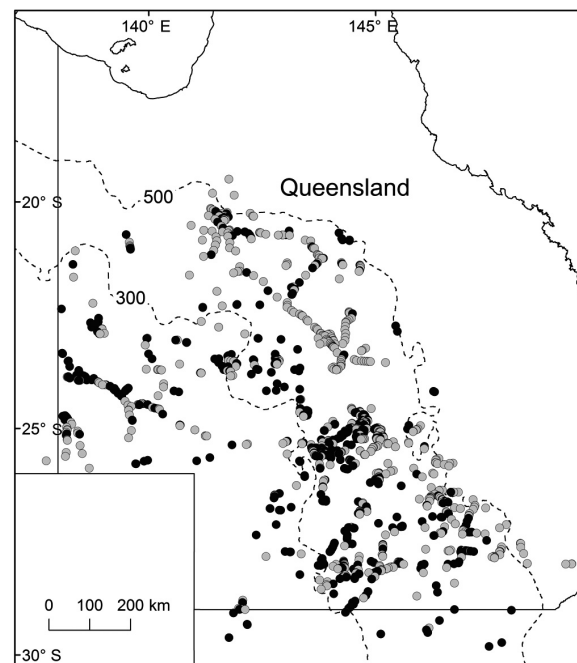

FIG. 1. Northeastern Australia study area, showing presence (black) and absence (gray) records of 45 candidate rare species. State borders (solid) and rainfall isohyets (mm, dashed) are indicated.

densities of only four species of large herbivores, all kangaroos in the genus *Macropus* (*M. fuliginosus*, *M. giganteus*, *M. robustus*, *M. rufus*). The historical record (Silcock et al. 2013) suggests that macropods were probably suppressed by the lack of available drinking water, predator pressure from dingoes, and Aboriginal hunting (Newsome 1975, Fensham and Fairfax 2008, Letnic et al. 2012).

Most of the study area is used for extensive cattle grazing but the eastern portion includes some sheep grazing, with relatively small areas occupied by conservation reserves mostly gazetted in the 1990s. The density of domestic livestock is greatly enhanced by an extensive network of artificial water points (James et al. 1999) and densities vary considerably between habitats and seasons. In the most productive habitats, such as tussock grassland, typical stocking rates are about 0.1 cattle equivalents/ha (Scattini et al. 1988).

Macropod densities have probably been enhanced by pastoral management (predator control, low levels of hunting, availability of water, and manipulation of habitat by clearing and grazing) and their densities decline across the aridity gradient from about 30 to 5 animals/km^2 (Pople and Grigg 2001). Feral and semi-domesticated goats also occur in high densities in the sandstone ranges and in southern parts of the study area (Fig. 1; Pople and Froese 2012).

Field surveys

Potentially rare plant species (nomenclature follows Bostock and Holland 2016) occurring in the drylands of northeastern Australia were assessed using herbarium data, published information and expert interviews (Silcock et al. 2014). In addition to currently listed species, those that were (1) known from <10 populations; (2) had not been collected in the study area in the past 20 yr; (3) likely to be a new or undescribed and restricted species; or (4) displayed an apparent declining population trend or a suspected threat, were identified as "candidate species" (Silcock et al. 2011). Species associated with permanent springs, some species thought to be rare but that were common, and species found in less than three populations during surveys were not included. The final list comprised 45 terrestrial plant species representing a range of habitats, life forms (Table 1), and variable geographic range extents.

A total of 1,372 surveys for the candidate species were conducted over 5 years between May 2010 and June 2015 and the results of these surveys for the threat status and habitat associations have been previously published (Silcock et al. 2014). Surveys encompassed a range of seasons, including the highest rainfall on record for large parts of the study area in 2010 and well above-average rainfall in 2011 and, for the north of the study area (Fig. 2) in 2009. The years 2006 and 2008 were dry years across most of the area, with extremely dry conditions returning across the study area in 2013. Initial searches were at sites of historical collections, guided by available information on habitat preferences and life history. At each site, habitat data was recorded and search effort quantified in terms of person hours and area searched (McDonald 2004), and whether the herbaceous vegetation was responding to recent rainfall was noted. Survey sites were haphazardly located adjacent to roads and tracks but targeted to the habitat preferences of species of interest. Because there were many species of interest, surveys were conducted across a broad range of habitats. As the surveys progressed, the habitat association of individual species became apparent and could be clearly defined (Table 1). While many of the 'rare' candidates were found to be abundant or common within their preferred habitat (Silcock et al. 2014) their distribution was always patchy suggesting a possibility that they may have declined with grazing.

Given temporal variability in plant germination and growth in arid environments (Holmgren et al. 2006), absence records were not included for annual or geophytic species when climatic conditions were unsuitable for their detection. At each location, the palatability of the target species was observed from the number of populations visited where grazing of the species in question was observed, and assigned to a category: ungrazed, no populations observed to be grazed during surveys; rarely grazed, evidence of grazing in <10% of populations; sometimes grazed, evidence of grazing in 11–50% of populations; frequently grazed, evidence of grazing in >50% of populations.

Correlation with water remote areas

The geographic range of each species was defined by a 50-km buffer around the minimum convex geometry that circumscribed the presence records of this survey as well as previous records extracted from herbarium collections.

The nearest permanent (contains water for >90% of the time on average) and semipermanent water (contains water for 70–90% of the time on average) from every survey location was determined. Permanent and semipermanent natural waterbodies (waterholes, springs, and rockholes) were mapped through interviews with long-term land managers (Fensham et al. 2011b). Bores were assumed to be permanent because most source artesian or reliable sub-artesian aquifers and were mapped from available imagery (Google Earth and Queensland Globe [*available online*])[6] and verified by the presence of round tanks, fenced earthen water-holding structures, and earthen water-holding structures positioned away from water courses. A coverage of dams, defined as semipermanent waters, was also employed (data *available online*).[7] Presence and absence records of the target plant

[6] https://www.business.qld.gov.au/running-business/support-assistance/mapping-data-imagery/maps/queensland-globe/about
[7] http://www.ga.gov.au/metadata-gateway/metadata/record/83134

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Table 1. Habitat, life form. and palatability of the 45 rare plant species included in the current study.

Species	Habitat	Life form	Palatability
Acacia ammophila	dune fields; gidgee woodlands	tree	frequently grazed
Acacia crombiei	wooded downs	tree	sometimes grazed
Acacia sp. (Ambathala C. Sandercoe 624)	residuals (gorges and creeklines)	tree	ungrazed
Actinotus paddisonii	spinifex sandplains	annual forb	ungrazed
Atriplex fissivalvis	residuals	annual forb	ungrazed
Atriplex lobativalvis	claypans and floodplains	annual forb	rarely grazed
Austrobryonia argillicola	Mitchell grass downs	geophyte	ungrazed
Austrochloris dichanthioides	sandy red earths	perennial grass	sometimes grazed
Caesia chlorantha	Mitchell grass downs	geophyte	ungrazed
Calandrinia sp. (Lumeah R.W. Purdie 2168)	residuals (barren plateaus)	annual forb	ungrazed
Digitaria hubbardii	sandy red earths	perennial grass	rarely grazed
Dodonaea intricate	residuals (barren plateaus)	shrub	rarely grazed
Elacholoma hornii	wetlands	annual forb	ungrazed
Eremophila woodiae	residuals (barren plateaus)	shrub	ungrazed
Eremophila stenophylla	residuals; gidgee toeslopes; Mitchell grass downs	shrub	frequently grazed
Euphorbia sarcostemmoides	residuals (barren plateaus)	shrub	ungrazed
Glinus orygioides	claypans in dune fields	annual forb	rarely grazed
Goodenia angustifolia	stony plains	perennial forb	rarely grazed
Goodenia atriplexifolia	residuals (barren plateaus)	perennial forb	rarely grazed
Grevillea kennedyana	residuals (stony hills)	shrub	ungrazed
Hakea maconochieana	residuals (barren plateaus)	shrub	ungrazed
Indigofera haematica	residuals (barren plateaus)	shrub	sometimes grazed
Indigofera oxyrachis	residuals (creeklines; toeslopes)	shrub	rarely grazed
Iseilema calvum	Mitchell grass downs	annual grass	rarely grazed
Ixiochlamys integerrima	limestone	perennial forb	sometimes grazed
Maireana cheelii	floodplains	annual forb	sometimes grazed
Maireana lanosa	dune fields	shrub	sometimes grazed
Oldenlandia spathulata	Mitchell grass downs	annual forb	ungrazed
Osteocarpum pentapterum	stony plains	annual forb	rarely grazed
Phyllanthus involutus	residuals; hard mulga	shrub	ungrazed
Ptilotus brachyanthus	sandy rises in Mitchell grass downs	annual forb	rarely grazed
Ptilotus maconochiei	residuals (scree slopes/boulder fields)	perennial forb	rarely grazed
Ptilotus remotiflorus	residuals (toeslopes)	perennial forb	rarely grazed
Rhaphidospora bonneyana	residuals (gorges and creeklines)	shrub	sometimes grazed
Rhyncharrhena linearis	sandy red earths and residuals	perennial forb	sometimes grazed
Ricinocarpos crispatus	residuals	shrub	rarely grazed
Sauropus ramosissimus	residuals	perennial forb	rarely grazed
Sclerolaena walkeri	floodplains	annual forb	rarely grazed
Sida argentea	riparian	perennial forb	frequently grazed
Sida asterocalyx	residuals (barren plateaus)	shrub	sometimes grazed
Solanum pisinnum	sandy red earths	perennial forb	ungrazed
Solanum versicolor	sandy red earths (soft mulga)	perennial forb	rarely grazed
Trachymene clivicola	residuals (scree slopes/boulder fields)	annual forb	rarely grazed
Urochloa atrisola	Mitchell grass downs	annual grass	rarely grazed
Xerothamnella parvifolia	residuals; gidgee toeslopes	shrub	frequently grazed

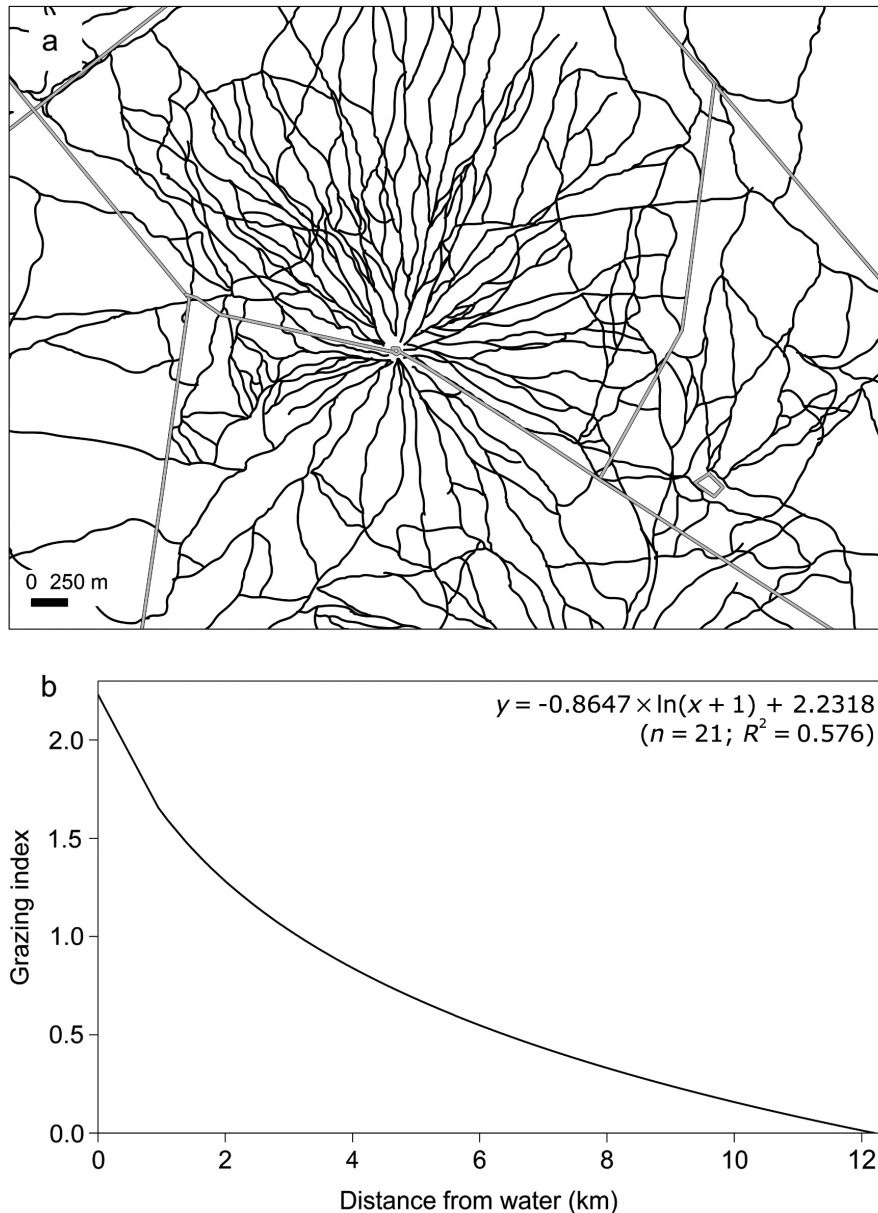$$y = -0.8647 \times \ln(x + 1) + 2.2318$$
$$(n = 21; \; R^2 = 0.576)$$

Fɪɢ. 2. (a) The pattern of cattle tracks emanating from a water point in the drylands of northeastern Australia with fence lines also indicated (−21.866, 143.178); (b) the relationship between distance to water and grazing index, as determined from dung (grey lines) counts (Fensham et al. 2010), employed in the current study.

species were overlain with locations of permanent and semipermanent water points, and intersected to give the distance of each water type from each record. In some cases there are fences between the locations and the mapped water point. However, there are macropods in the landscape that traverse fences, access can be available through gates and not all fences are functional. Thus fences were ignored for this analysis.

Grazing is focused around water points in the drylands of Australia (Fig. 2a; Fensham and Fairfax 2008). For cattle a relationship between distance to water and grazing activity has been established using dung counts

(Fig. 2b; Fensham et al. 2010). These data suggests that grazing activity is greatest within about 3 km from water and then declines gradually to zero at about 12 km. This relationship is generally compatible with assessments of cattle grazing activity from other Australian drylands (Fensham and Fairfax 2008). It also provides a reasonable approximation to sheep grazing activity, which is strongly focused within 3 km of water points (Fensham and Fairfax 2008). The grazing pattern of the dominant macropod in drylands, the red kangaroo (*M. rufus*) exhibits little pattern up to 7 km from water but beyond this distance grazing activity is constrained during dry

seasons (Fensham and Fairfax 2008). It is estimated that the grazing pressure of a red kangaroo standardized to body mass is 44% of a sheep (Munn et al. 2013).

This function was employed in the current study to convert distance to water to a grazing index, with a floor value of zero for all records occurring further than 12 km from water. This function underestimates grazing activity in the heavily disturbed area within 400 m of a permanent water point (Fensham et al. 2010), but only 4.5% of the samples in the current study are within this distance. Given the variations in herbivores, fences, management, history, and habitat mosaics, the grazing index is a coarse indication of the history of grazing intensity at any given point. Developing an accurate measure of grazing history for the large number of survey sites represented by this study would be an extremely difficult task. This study is predicated on the assumption that the position of water points is a powerful determinant of grazing intensity and history, and that if grazing is an important determinant of dryland plant species distribution it will be reflected by this large data set representing multiple species.

The presence and absence records of each species were used to build binomial logistic regression models designed to predict the presence of species in relation to grazing index and mean annual rainfall. Absence records outside a species habitat and geographic range were excluded. Rainfall was included in these models to control for the effect of climatic drivers of species distribution within their habitats. To test for spatial autocorrelation in model residuals, spatial spline correlograms of the residuals of each model were estimated using the R package ncf. Based on these correlograms, all cases where the 95% confidence interval of the autocorrelation coefficient did not overlap zero were identified as an indication of statistically significant spatial autocorrelation. Where significant spatial autocorrelation between the residuals and the grazing activity effect were identified the chance of a type I error increases (Legendre 1993).

Results

We conducted >1,000 h of targeted searches for the 45 target species. A total of 2,084 populations were found. Distances to permanent or semipermanent water ranged from 0.00 km to 99.54 km. There were inherent differences in distance to water between habitats with the Sandy rises in Mitchell grass downs having the shortest distance to water (mean, 2.26 km; range, 0.00–6.15 km) and dune fields having the longest distance to water (mean, 19.27 km; range, 0.29–53.71 km). The analysis of semipermanent water points generated fewer significant results than the analysis of permanent water points (Appendix S1: Table S1).

Of all the 45 rare species, the perennial forb *Solanum versicolor* was the only species where the presence records were associated with lower grazing activity around permanent water points than the absence records (Table 2). This species was observed to be only rarely grazed. Grazing index and mean annual rainfall were correlated (Table 2) for this species and the residuals in the model were not autocorrelated (Appendix S1: Fig. S1). The marginal association of the presence records with low grazing index values for this species is not particularly apparent with a spatial representation of the data (Fig. 3)

The modeling indicates that the presence records for three species (*Caesia chlorantha*, *Glinus orygioides*, and *Ixiochlamys integerrima*) were associated with greater grazing activity than the absence records (Table 2). Grazing index and mean annual rainfall were not significantly correlated for any of these three species (Table 2) but there was a significant spatial autocorrrelation for *Ixiochlamys integerrima* at between 40 and 60 km scale (Appendix S1: Fig. S1).

Mean annual rainfall was a significant determinant of presence for 12 of the 45 species with eight of those species more likely to occur in low rainfall areas of their geographic range than high rainfall areas (Table 2).

Discussion

There is no evidence from this study that livestock grazing is a substantial cause of rarity for the flora of drylands in northeastern Australia. Only one of 45 (2.2%) rare plant species included in this study had a statistically significant association with distance to water (Table 2). The marginal effect for this species (Fig. 3) may be a product of a trend in abundance with mean annual rainfall because this variable was correlated with the grazing index (Table 2). Field observations indicate that this species is rarely grazed (Table 1). The 44 rare plant species that were not associated with low grazing activity include 29 with a perennial life form, and four species observed to be frequently grazed and nine sometimes grazed (Table 1).

The analysis here was founded on the assumption that there is a direct relationship between distance to water and grazing pressure within individual habitats. However there are other factors that affect grazing pressure (Pringle and Landsberg 2004). In our study area, the impact of macropods will be important because their density has probably increased with European management, particularly in the east of the study area (Silcock et al. 2013) and their association with water points is much weaker than domestic livestock (Montague-Drake and Croft 2004, Fensham and Fairfax 2008).

Some species may have been eradicated by grazing and their presence records are too few to discriminate a grazing response. Based on their sample size (Table 2), there are two likely candidates. The first is *Rhyncharrhena linearis*, a perennial vine that is very rare in our study area, which is sometimes grazed by livestock. In other grazed regions within its distribution, *Rhyncharrhena linearis* is also rare and considered grazing sensitive (Parsons 2004).

TABLE 2. Results of GLM models predicting the presence/absence of plant species in relation to distance to water and mean annual rainfall for permanent water points.

Species	n (n present)	Grazing activity index	Mean annual rainfall	R
Acacia ammophila	28 (18)	-0.73 ± 1.16 (0.527)	0.04 ± 0.04 (0.337)	-0.002
Acacia crombiei	19 (10)	-0.26 ± 1.32 (0.846)	0.03 ± 0.04 (0.545)	-0.096
Acacia sp. (Ambathala C. Sandercoe 624)	27 (12)	-0.22 ± 0.60 (0.709)	0.02 ± 0.01 (0.159)	-0.535
Actinotus paddisonii	60 (11)	0.94 ± 0.79 (0.233)	-0.02 ± 0.01 (0.087)	-0.167
Atriplex fissivalvis	15 (6)	-0.81 ± 1.19 (0.496)	0.01 ± 0.01 (0.612)	-0.340
Atriplex lobativalvis	71 (54)	1.78 ± 1.27 (0.159)	0.05 ± 0.02 (0.035)	0.001
Austrobryonia argillicola	127 (19)	0.00 ± 0.53 (0.998)	-0.01 ± 0.00 (0.000)	0.152
Austrochloris dichanthoides	17 (12)	-1.12 ± 1.10 (0.309)	0.00 ± 0.01 (0.957)	-0.837
Caesia chlorantha	129 (13)	2.28 ± 0.94 (0.016)	-0.03 ± 0.01 (0.036)	0.322
Calandrinia sp. (Lumeah R.W. Purdie 2168)	115 (63)	0.69 ± 0.42 (0.100)	-0.02 ± 0.00 (0.000)	-0.198
Digitaria hubbardii	65 (34)	-0.19 ± 0.75 (0.796)	-0.03 ± 0.01 (0.001)	0.122
Dodonaea intricata	27 (9)	-1.51 ± 1.62 (0.351)	0.05 ± 0.02 (0.007)	-0.045
Elacholoma hornii	20 (7)	0.22 ± 1.09 (0.842)	-0.01 ± 0.01 (0.278)	0.329
Eremophila stenophylla	27 (20)	-1.47 ± 1.03 (0.155)	-0.01 ± 0.01 (0.169)	0.258
Eremophila woodiae	13 (7)	-2.76 ± 1.94 (0.156)	-1.82 ± 1.36 (0.181)	0.594
Euphorbia sarcostemmoides	137 (44)	0.47 ± 0.39 (0.229)	-0.01 ± 0.00 (0.029)	-0.003
Glinus orygioides	21 (12)	6.56 ± 2.99 (0.028)	-0.07 ± 0.03 (0.039)	0.583
Goodenia angustifolia	28 (9)	0.95 ± 0.89 (0.285)	-0.01 ± 0.00 (0.265)	**-0.874**
Goodenia atriplexifolia	61 (37)	-0.45 ± 0.54 (0.403)	0.01 ± 0.01 (0.323)	-0.336
Grevillea kennedyana	11 (5)	2.04 ± 2.09 (0.330)	0.14 ± 0.19 (0.444)	0.103
Hakea maconochieana	55 (13)	0.29 ± 0.74 (0.697)	-0.02 ± 0.01 (0.009)	**0.801**
Indigofera haematica	11 (7)	0.92 ± 1.19 (0.438)	-0.01 ± 0.03 (0.777)	0.127
Indigofera oxyrachis	33 (15)	-1.64 ± 1.16 (0.157)	0.00 ± 0.01 (0.943)	0.002
Iseilema calvum	78 (8)	-1.39 ± 0.96 (0.145)	-0.02 ± 0.02 (0.322)	-0.523
Ixiochlamys integerrima	20 (13)	4.57 ± 2.23 (0.041)	-0.08 ± 0.04 (0.035)	0.418
Maireana cheelii	16 (6)	0.01 ± 1.02 (0.989)	-0.02 ± 0.02 (0.272)	0.328
Maireana lanosa	41 (26)	1.86 ± 1.55 (0.230)	-0.02 ± 0.01 (0.056)	0.000
Oldenlandia spathulata	22 (6)	2.50 ± 1.90 (0.188)	0.06 ± 0.04 (0.185)	**0.954**
Osteocarpum pentapterum	24 (15)	-0.72 ± 0.88 (0.413)	0.00 ± 0.01 (0.762)	-0.162
Phyllanthus involutus	27 (15)	2.93 ± 1.77 (0.097)	0.11 ± 0.05 (0.033)	-0.618
Ptilotus brachyanthus	25 (3)	0.24 ± 1.83 (0.898)	-0.09 ± 0.05 (0.074)	0.109
Ptilotus maconochiei	24 (5)	-0.38 ± 0.86 (0.659)	0.01 ± 0.01 (0.369)	0.274
Ptilotus remotiflorus	60 (45)	0.27 ± 0.68 (0.692)	0.00 ± 0.00 (0.370)	0.011
Rhaphidospora bonneyana	38 (16)	0.91 ± 0.70 (0.197)	0.00 ± 0.01 (0.598)	-0.310
Rhyncharrhena linearis	49 (3)	0.60 ± 1.36 (0.660)	0.00 ± 0.01 (0.774)	**0.865**
Ricinocarpos crispatus	28 (11)	-2.13 ± 1.29 (0.098)	0.08 ± 0.04 (0.035)	0.484
Sauropus ramosissimus	15 (8)	-2.00 ± 1.87 (0.285)	-0.01 ± 0.01 (0.100)	0.545
Sclerolaena walkeri	43 (33)	-1.23 ± 0.67 (0.066)	0.01 ± 0.01 (0.127)	0.001
Sida argentea	11 (7)	-0.98 ± 1.65 (0.551)	0.02 ± 0.03 (0.427)	0.532
Sida asterocalyx	42 (25)	-1.44 ± 0.93 (0.124)	0.00 ± 0.01 (0.857)	-0.506
Solanum pisinnum	17 (8)	1.43 ± 1.26 (0.258)	0.03 ± 0.02 (0.227)	-0.836
Solanum versicolor	23 (6)	-5.43 ± 2.60 (0.037)	-0.01 ± 0.02 (0.801)	**-0.866**
Trachymene clivicola	22 (6)	1.01 ± 0.69 (0.146)	0.00 ± 0.01 (0.848)	-0.329
Urochloa atrisola	53 (18)	-0.39 ± 0.82 (0.636)	0.00 ± 0.01 (0.866)	0.027
Xerothamnella parvifolia	104 (76)	-0.24 ± 0.53 (0.649)	-0.01 ± 0.00 (0.001)	-0.086

Notes: Values are coefficients (mean $\pm$ SE) with *P* values in parentheses. Models where the residuals are autocorrelated are identified by the range of distance where the 95% error bounds do not overlap with zero (see Appendix S1: Fig. S1). Spearman's rank correlation coefficient (*R*) between grazing activity and mean annual rainfall are presented with values significant at *P* < 0.05 highlighted in boldface type.

In central desert regions of Australia on land managed by indigenous people where domestic livestock are sparse, this species is relatively common (D. Albrecht and P. Latz, *personal communication*). The second is *Ptilotus brachyanthus*, which occurred in the habitat with the lowest values of distance to water and was only present in 3 out of 25 sites (Table 2). Like *Rhyncharrhena*, this species may be grazing sensitive but the effect of grazing was not revealed by the analysis because there was insufficient discrimination in the data set. Field observations indicate that the perennial species *Acacia ammophila*, *Eremophila stenophylla*, *Sida argentea*, and *Xerothamnella parvifolia*
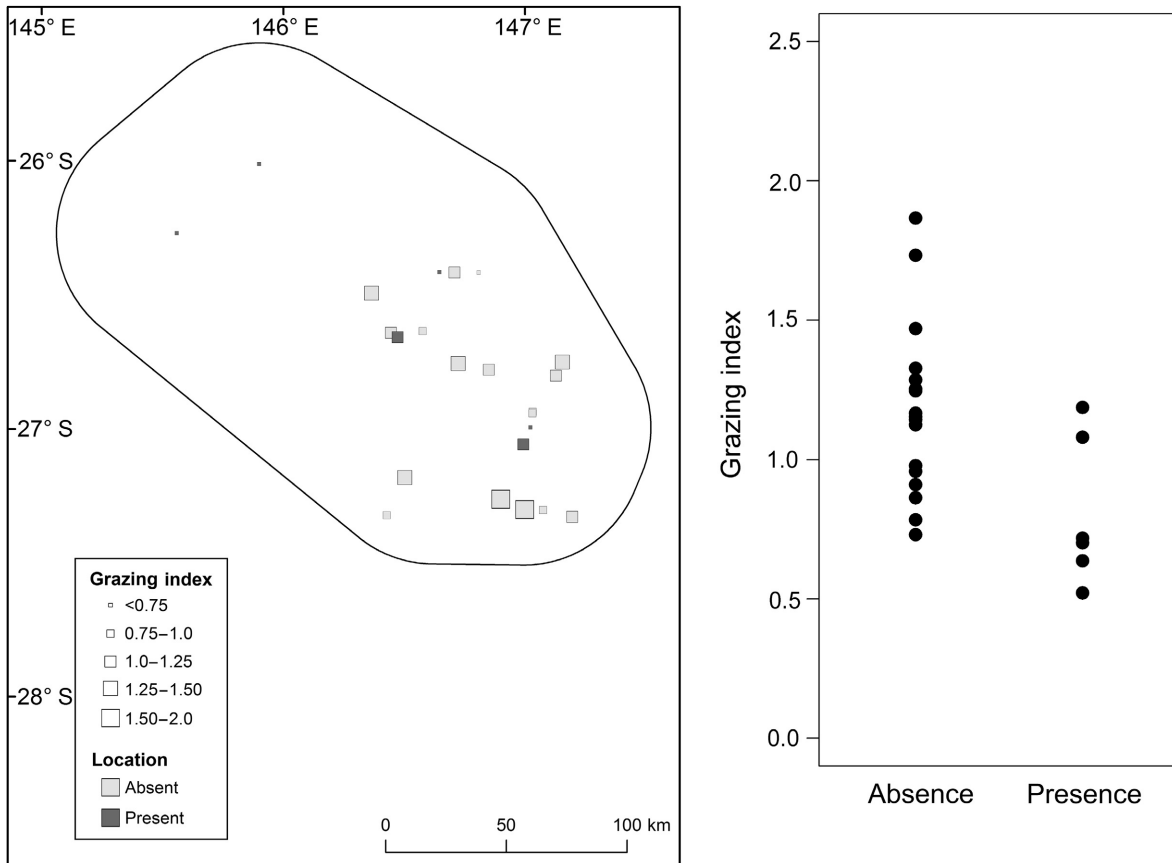
FIG. 3. The geographic range of *Solanum versicolor* (line) with presence (dark gray) and absence records (light gray) from the current survey scaled according to the grazing index with the upper limit of each grazing index threshold identified in the legend. The right hand graph indicates the presence and absence records in relation to distance to water.

are frequently grazed by domestic livestock, feral goats, and native herbivores (Table 1) and recruitment is rare. Although they have persistent populations, palatable perennials may decline to extinction over long timescales due to lack of recruitment. This has been suggested for other long-lived palatable species in drylands (Lange and Graham 1983, Hunt 2001, Denham and Auld 2004) and further population studies on these species are warranted.

The Australian continent has been subject to a dramatic increase in grazing pressure since the advent of pastoralism in the nineteenth century. Our study provides quantitative support for emerging and surprising evidence of the resilience of the Australian dryland flora to this amplification in herbivory (Fensham et al. 2010, 2011*a*, 2014, Silcock and Fensham 2013, 2014). This study also provides support for the theory purporting disequilibrium between herbivore pressure and plant resources in dryland ecosystems. This resilience has been partly attributed to the high proportion of ephemeral species that can set seed rapidly after unpredictable rainfall events that characterize the climate of the region (Silcock and Fensham 2013). With low livestock densities, these species are able to complete their lifecycle before being affected by grazing. An important exception may be palatable perennial

species. Their long-term population trends should be monitored and the dynamics of their life-cycles investigated, particularly in relation to the boom and bust cycles of rainfall that are critical determinants of the ecology of drylands (Holmgren et al. 2006).

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1911/full

Data Availability

Data are available from UQ eSpace, the University of Queensland's institution repository, at https://doi.org/10.14264/uql.2019.294