

RESEARCH ARTICLE

Ants respond more strongly to grazing than changes in shrub cover

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Abstract

Increases in the cover or density of woody plants (encroachment) and overgrazing by European livestock are 2 major drivers of ecosystem structure and function in drylands and are often associated with land degradation. Although the effects of encroachment and overgrazing on vascular plants are relatively well known, little is known about their effects on arthropods such as ants. We examined ant community composition at sites ranging in shrub cover in a wooded dryland in eastern Australia, testing the notion that increasing shrub cover and grazing intensity would alter ant assemblages and functional group composition. We used ants because they are abundant, diverse, and respond to small-scale environmental changes. Increasing shrub cover had no effect on ant richness, diversity, or evenness but increased the abundance of Subordinate Camponotini. Larger shrubs tended to have greater ant richness, and abundance of Cold Climate Specialists, but fewer Generalized Myrmicinae and Hot Climate Specialists. More intense grazing was associated with greater ant richness, diversity, and evenness; a greater abundance of Hot Climate Specialists and Dominant Dolichoridae; and lower abundance of Subordinate Camponotini. Our study indicates that changes in grazing intensity had stronger effects on ant richness than any increase in shrub cover. The effects of grazing likely resulted from changes in soil surface complexity such as barer ground associated with grazing-induced degradation.

KEYWORDS

ant community, complexity, drylands, *Formicinae*, grazing, livestock

1 | INTRODUCTION

The proliferation of woody plants and their encroachment into open woodlands and grasslands (shrub encroachment, woody encroachment, or thickening) is a global phenomenon characterized by an increase in the cover and density of shrubs at the expense of herbaceous plants (Eldridge et al., 2011). Encroachment is thought to be driven by a combination of factors including increased concentrations of atmospheric CO₂, altered fire regimes, and anthropogenic activities such as overgrazing by domestic livestock (Roques, O'Connor, & Watkinson, 2001; van Auken, 2009). Dense encroachment has profound effects on woodland and grassland ecosystems by simplifying the structure and composition of vegetation, compared with the original grassland or open woodland (Maestre, Eldridge, & Soliveres, 2016). Reductions in grass cover and increases in vertical complexity associated with encroachment can alter the abiotic and biotic environment beneath shrub canopies by enhancing soil carbon and nitrogen pools (Howard, Eldridge, & Soliveres, 2012), altering soil structure and

stability (Daryanto & Eldridge, 2010), reducing fluctuations in radiation and temperature, or increasing leaf litter, which alters habitat for plants and animals (Sirami, Seymour, Midgley, & Barnard, 2009). Shrublands, however, are often severely overgrazed by livestock, and the negative effects of grazing on shrubland-dependent plants and animals are often attributed to the shrubs themselves (Eldridge, Soliveres, Bowker, & Val, 2013; Soliveres et al., 2014; van Auken, 2009).

The notion that shrubs at high densities are a sign of land degradation and might lead to reductions in biodiversity seems largely at odds with global empirical evidence that woody plants create favourable microsites beneath their canopies and increase understory vascular plant diversity (Eldridge & Soliveres, 2014). Global studies suggest that vertebrate abundance and diversity increase with increasing shrub cover at relatively low levels of encroachment but may decline at high levels. For example, in the Kalahari Desert, the small-spotted genet (*Genetta genetta*), yellow mongoose (*Cynictis penicillata*), and bat-eared fox (*Otocyon megalotis*) showed unimodal responses to increasing shrub encroachment, reaching maximum abundance at about 20%

shrub cover (Blaum, Rossmannith, Schwager, & Jeltsch, 2007). In a South African savanna, local bird species richness increased with encroachment, reaching a maximum at cover levels of about 40% (Sirami et al., 2009), consistent with conceptual models from eastern Australia (Eldridge & Soliveres, 2014). Similarly, Rolo, Rivest, Lorente, Kattge, and Moreno (2016) demonstrated that plant species richness peaked at about 40% shrub cover in an Iberian grassland.

Compared with rodents, large mammals, and birds, which are known to respond to landscape-level change in habitat structure and complexity (Blaum, Seymour, Rossmannith, Schwager, & Jeltsch, 2009), the effects of shrub encroachment on ground-dwelling arthropods such as ants are poorly known. Arthropods are a major food component for larger fauna and provide a range of critical ecosystem services such as pollination, seed dispersal, decomposition, and nutrient cycling (Eisenhauer, Sabais, Schonert, & Scheu, 2010). Ants, in particular, are important ecosystem engineers as their nests modify the surrounding environment, making resources available to other biota, and promote nutrient cycling and increase soil water infiltration (Jouquet, Dauber, Lagerlöf, Lavelle, & Lepage, 2006). These functions are critically important in drylands where resources are patchily distributed and water and soil nutrients are generally low (Noy-Meir, 1973).

We examined the effects of shrub encroachment, which is often regarded as an indicator of landscape degradation (Eldridge & Soliveres, 2014) on ground-active ants in an environment where they comprise a major component of the terrestrial biota. Ants are useful indicators of ecosystem health because they are abundant, diverse, and react to small-scale environmental changes (Gómez & Abril, 2011). Ant diversity, abundance, and functional group composition are influenced by plant richness and structure but can also be influenced by overgrazing, as many shrublands are degraded and show evidence of severe overgrazing. Thus, changes in plant community structure associated with increasing shrub density would be expected to elicit substantial changes in their community structure (Retana & Cerdá, 2000). Increases in bare soil associated with grazing would be expected to influence ant community composition because bare soil increases foraging efficiency and is easier for some species to monopolize (Gibb & Parr, 2010).

We tested the proposition that changes in shrub cover associated with encroachment would alter ant assemblages. We predicted that ant richness and diversity would follow a unimodal response with increasing shrub cover as moderate levels of shrub cover would increase habitat complexity and niche availability, consistent with model predictions (*sensu* Eldridge & Soliveres, 2014; Hypothesis 1). Moderate levels of shrub encroachment have been shown to increase ant diversity and composition in the temperate seminatural grasslands of western Carpathians (Wieżik, Svitok, Wierzchová, & Dovčiak, 2013). We predicted that the abundance of Subordinate Camponotini would increase with high levels of shrub cover as *Camponotus* species are known to prefer shrub and tree microsites (Gano & Rogers, 1983; Hypothesis 2). We predicted that larger shrubs would increase the abundance of Cold Climate Specialists, which prefer cooler microsites (Debus, King, & House, 2007), but reduce the abundance of Hot Climate Specialists and Generalized Myrmicinae, which prefer hot and open environments, respectively (Andersen, 1991; Hypothesis 3). Because historic overgrazing is a major driver of shrub encroachment

(Roques et al., 2001; van Auken, 2009), and its effects are also confounded with shrub cover (Eldridge et al., 2013), we were also interested in exploring how grazing intensity might influence ant assemblage and composition over a gradient in shrub encroachment. We hypothesized that higher grazing intensity would increase the abundance of Dominant Dolichoderinae and Hot Climate Specialists as these functional groups prefer bare soil microhabitats (Andersen, 1995; Hypothesis 4).

2 | METHODS

2.1 | The study area

Our study was conducted in eastern Australia (30.18° to 32.64°S, 144.30°–145.29°E), west of the town of Cobar. The climate in the study region is semiarid, with rainfall varying from 278 to 353 mm (BOM, 2015). Summers are hot and dry with average maximum temperatures of 34.5 °C in January, and winters are cool with average minimum temperatures of 4.7 °C in July. The dominant landforms vary from lowlands and rolling downs to sandplains with low dunes. Soils are typically calcareous red earths with loamy and sandy-loam surface textures (Ayers et al., 2001). Many of the areas have been encroached by native shrubs including *Eremophila mitchellii*, *Eremophila sturtii*, *Senna artemisioides*, and *Dodonaea viscosa* ssp. *angustissima*. Shrubs have always been a part of these systems but, over the last century, have encroached into open areas as result of overgrazing, lack of wildfire, and, potentially, increased levels of atmospheric CO₂ (Eldridge & Soliveres, 2014).

2.2 | Site establishment and measurement of environmental variables

Our study was conducted at 35 sites representing a gradient in shrub cover from low (1%) to high (42%) and under two levels of grazing: low and moderate. The full range of shrub cover values occurred at sites under both low grazing moderate grazing (Figure S1). Thus, there was no evidence of confounding between shrub cover and grazing intensity. The highest level of shrub cover (42%) represents the upper level of shrub encroachment in eastern Australia (Eldridge et al., 2013). At each site, we established a 2 ha (200 × 100 m) plot with a 100-m buffer of similar shrub cover around each site. Sites ranged from 1.2 to 5.4 km from water (median: 3.1 km) and had comparable fire histories and similar soil types (Ayers et al., 2001).

At each site, we measured the cover, height, and distance between 20 shrubs encountered along five 100-m transects using the Wandering Quarter method (Ayers et al., 2001). Only woody plants between 0.3 and 4 m tall were measured. Measurements of the distance between individual shrubs allowed us to calculate shrub density. Shrub cover was calculated by measuring two diameters of each shrub canopy, through the centre, estimating the area to be an ellipse.

Grazing intensity is a major driver of shrub encroachment (Roques et al., 2001) and known to have mixed effects on ant richness and composition (Hoffmann & Andersen, 2003). To determine how livestock grazing affected ant richness and composition, we used two measures of grazing intensity: (a) the proximity to permanent water and (b) a

qualitative score, categorized as either low or moderate grazing. Proximity to water has been used as a proxy for grazing intensity because livestock such as cattle and sheep graze more intensively close to water, particularly during droughts (Fensham & Fairfax, 2008). Proximity to water was measured as the distance from the centre of each site to the nearest water point using a global positioning system. The qualitative score was based on the presence of physical, grazing-induced disturbances such as livestock hoof prints, the density of tracks, and the presence and abundance of livestock dung. We also noted the presence of livestock at our sites, but as all sites were grazed, so this was not very informative. To complement the qualitative measure of grazing intensity, we collected data on the morphology of the soil surface in order to calculate a soil stability index (Tongway, 1995). This soil stability index has been shown to be correlated with grazing-induced disturbance and empirical measures of livestock activity (Eldridge, Delgado-Baquerizo, Travers, Val, & Oliver, 2016) and has been used widely to examine surface disturbances (eg, Ata Rezaei, Arzani, & Tongway, 2006). The soil stability index is based on an assessment of six soil surface attributes: soil surface resistance and stability, the cover of biocrusts, the cover of erosion, cover of eroded material, and litter cover. At each site, these six attributes were assessed within ten 0.25-m² quadrats along a 100-m transect. Each attribute was scored from 1 to 4 (or 5), with a higher score corresponding to a more stable surface. The soil stability index was then calculated as the arithmetic mean of the values of the six attributes divided by the maximum possible score (see Table S1 for specific analytical methods). The stability index was greater (a more stable surface) under low than moderate levels of grazing (ANOVA: $F_{1,33} = 7.90, p = .008$) providing support for our qualitative measure of grazing intensity. Notwithstanding the qualitative nature of the grazing intensity score (low, moderate), we used it in any analyses because land managers are more familiar with this type of terminology.

To assess how shrub encroachment influences ant richness and community composition, we measured six environmental attributes at each site that provide a measure of landscape organization, surface complexity, and soil type. These were fetch length (m), litter cover (%), bare soil cover (%), biological crust cover (biocrust; %), total number of logs, and soil texture. Fetch length is the average distance between habitat patches and is a useful measure of landscape organization (Ludwig, Tongway, Hodgkinson, Freudenberger, & Noble, 1996). Habitat patches included perennial grasses >2-cm diameter at the base, logs >10 cm in diameter, and tree and shrub hummocks. These hummocks are mounds of accumulated soil that surround the trunks of trees and shrubs. Fetch length was measured over a 100-m transect, orientated down the slope, using the line-intercept method. Logs >10 cm in diameter within two 4 by 200 m transects at each site.

Surface complexity affects ant richness and composition by altering resource availability, foraging behaviour, interspecific competition, and predation pressure (Gibb & Parr, 2010). Habitat features were assessed in the two transects. Cryptic ant species forage within leaf litter, but Hot Climate Specialists and Opportunists prefer bare soil (Andersen, 1991; Bestelmeyer & Wiens, 1996; Hoffmann & Andersen, 2003). Biocrust cover is important for increasing soil stability, reducing soil surface temperature, and reducing soil moisture (Li, Jia, Chen, Huang, & Zhang, 2011), which can all affect ant locomotion, foraging

strategies, and nest distribution. Log density and distribution likely affect ant communities by altering soil surface complexity and seed availability, as logs accumulate leaf litter, seeds, and sediment around their base. Soil texture (the percentage of sand, silt, and clay in the soil) was determined using the bolus technique (Tongway, 1995). Soil texture can directly affect ant nest distribution and indirectly affect ant communities through resource availability such as seed abundance by influencing plant richness and composition.

2.3 | Sampling the ant fauna

At each site, we sampled the ant fauna using 10 pitfall traps, 10 cm deep × 6 cm wide, left open for 10 consecutive nights during the spring and summer of 1999 to 2000. Traps were separated by distances of about 10 m. Pitfall traps were arranged in a two by five grid and buried with the top flush with the soil surface. Traps were filled with a mixture of monoethylene glycol and ethanol (2:1) to preserve specimens and reduce evaporation. A plastic plate mounted 10 cm above each trap prevented the ingress of rain. Ants were identified to morphospecies and functional groups by experts.

2.4 | Data set

The ant dataset included ant species abundance and functional group data pooled at the trap level. We calculated ant abundance, richness (S), diversity, and evenness using the DIVERSE function in PRIMER 6 + PERMANOVA (Anderson, Gorley, & Clarke, 2008). The functional group dataset included the total abundance of ant functional groups: Cold Climate Specialists, Dominant Dolichoderinae, Generalized Myrmicinae, Hot Climate Specialists, Opportunists, Specialist Predators, and Subordinate Camponotini. The *Monomorium* and *Tetramorium* genera were excluded from the functional group dataset as both genera are difficult to identify to species and their functional group was unknown. Similarly, the functional group Cryptic Species was excluded because of low abundance across all study sites.

2.5 | Statistical analysis

Our environmental dataset included the two shrub attributes (height and cover), two grazing attributes (proximity to water and intensity) and six environmental attributes (fetch length, litter, bare soil and biocrust cover, log density, and soil texture). Shrub density was not included as it was highly correlated with shrub cover.

We used a two-stage approach to analyse the data. In Stage 1, we used a generalized linear model (GLM) with a Poisson (log link) distribution to determine the effects of shrubs, grazing, and the environmental attributes on ant richness, diversity, and evenness separately using R base package (R Core Team, 2015). Each model contained the two shrub attributes, two grazing attributes, and one environmental attribute, either average fetch, litter, bare soil, biocrust, logs, or soil texture. Environmental data were standardized (z-transformed) prior to analyses. Soil texture was the only categorical data. We used the second-order Akaike information criterion (AICc) in the package MuMIn (Barbón, 2015) to determine the best model fit. Models within two units of the lowest AIC were deemed the best fit and were checked for heterogeneity and independence using the plot function as well as

overdispersion using the *anova* function. For each top model, coefficients were plotted with their 95% confidence interval.

In Stage 2, we used multivariate generalized linear models (*manyglm*) to explore how shrubs, grazing, and environmental attributes influence functional group composition using R package *Mvabund* (Wang, Naumann, Wright, & Warton, 2015). Similar to Stage 1, we modelled functional group abundance against the two shrub attributes, two grazing attributes, and one of the six environmental attributes. We used the Akaike information Criterion (AIC) to determine the model with the best fit. Models were checked for heterogeneity and independence using the *plot* function as well as overdispersion using the *anova.manyglm* function. Post hoc tests were conducted using the function *manyglm* to determine the response of individual functional group to shrub, grazing, and environmental attributes using adjusted *p* values. We plotted functional group coefficients with bootstrapped 95% confidence intervals for each top model.

To determine which genera were driving changes in functional group composition, we used GLM with a Poisson distribution in R base package (R Core Team, 2015). Coefficients, with bootstrapped 95% confidence intervals were used to identify the response of individual functional groups to changes in environmental variables. Genera from these functional groups were modelled separately against environment variables from the top functional group model. We used a one-way ANOVA to determine the effect of environmental variables on genera abundance. We then produced statistical predictor models on genera using genera average response and 95% CI.

3 | RESULTS

We recorded a total of 146,826 ants from 28 genera, 117 species, and 8 functional groups. *Monomorium* was the most diverse ant genus with 18 species, followed by *Iridomyrmex* with 15 species and *Meranoplus* with 12 species. *Iridomyrmex* accounted for 89% of total ant abundance. Ant richness ranged from 19 to 45 species across our sites.

3.1 | Models of ant species richness, diversity, and evenness

Shrub cover and height, grazing intensity, proximity to water, and cover of bare soil explained 35% of the variance in ant richness over the shrub gradient (Table S2). A similar model, but excluding the cover of bare soil and including fetch length, explained 21% of the variance in ant diversity (Table S3). Increasing the cover of bare soil was associated with reduced ant species richness (Figure 1). Overall, we found no evidence to support our first hypothesis that either richness or diversity (Figure 2) exhibited a unimodal response to increasing shrub cover.

3.2 | Ant community structure

The abundance of Subordinate Camponotini increased with increasing shrub cover, consistent with our second hypothesis, but all remaining functional groups showed no significant response to shrub cover (Figure 3; Table 1). The increase of Subordinate Camponotini was driven largely by members of the genera *Camponotus*

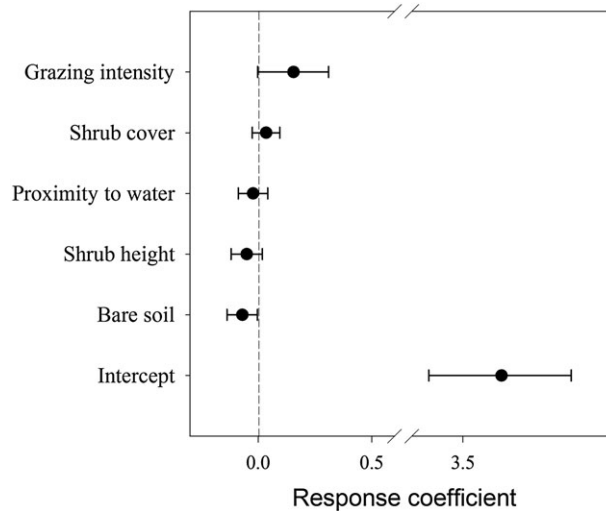


FIGURE 1 Ant richness model ($\pm 95\%$ CI) in relation to grazing intensity, biocrust cover, proximity to water, shrub height, and the cover of bare soil

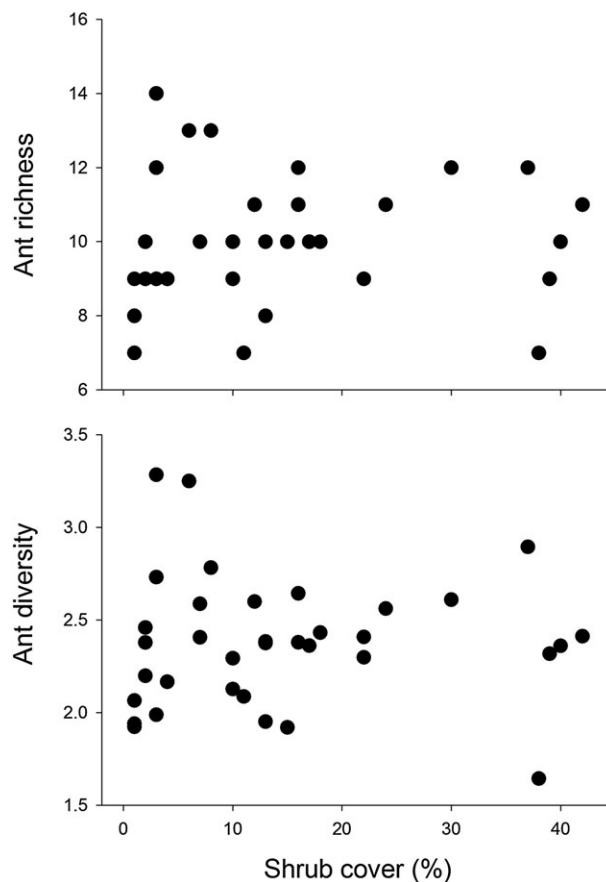


FIGURE 2 Scatterplot of ant richness and diversity in relation to shrub cover (%)

($\chi^2_{1,33} = 332.12$, $p < .001$) and *Polyrhachis* ($\chi^2_{1,33} = 46.34$, $p < .001$). Contrary to prediction, we found that Cold Climate Specialists and Dominant Dolichoderinae were unaffected by shrub cover. Functional groups showed mixed responses to shrub height. The abundance of Cold Climate Specialists increased, whereas Generalized Myrmicinae and Hot Climate Specialists declined, with increasing

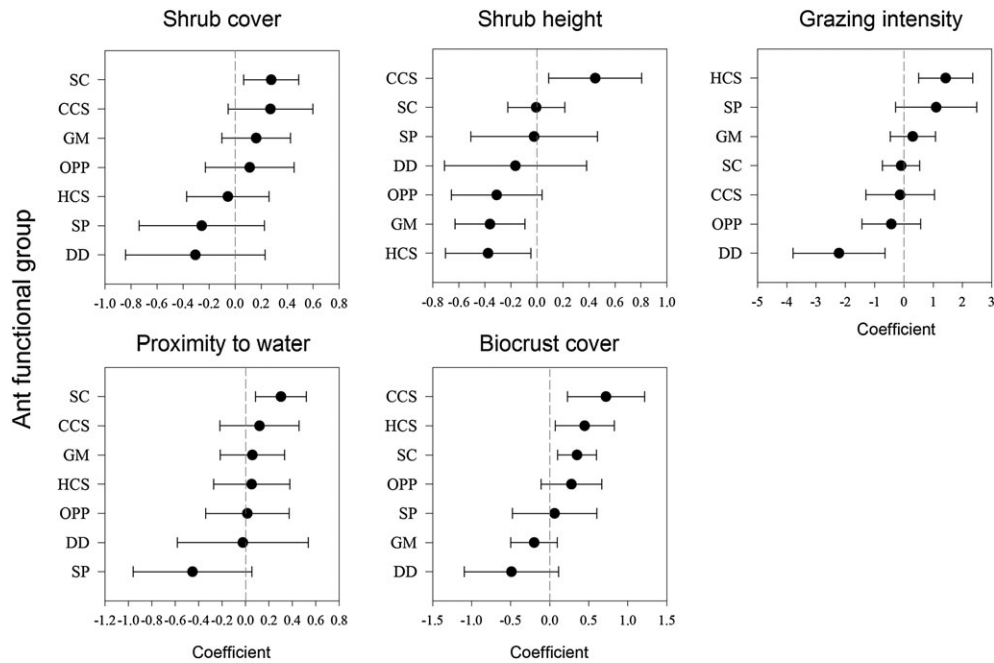


FIGURE 3 Functional group model coefficients ($\pm 95\%$ CI) in relation to the five environmental variables from the top functional group model: shrub cover, shrub height, grazing intensity, proximity to water, and biocrust cover. Functional groups include CCS = Cold Climate Specialists; DD = Dominant Dolichoderinae; GM = Generalized Myrmicinae; HCS = Hot Climate Specialists; OPP = Opportunists; SP = Specialist Predators; SC = Subordinate Camponotini

TABLE 1 Summary of the response of different functional groups to environmental attributes in the top functional group model

Environmental attribute	Functional group	Response
Shrub cover (%)	Subordinate Camponotini	Increase
Shrub height (m)	Cold Climate Specialist	Increase
	Hot Climate Specialist	Decrease
	Generalized Myrmicinae	Decrease
Grazing intensity	Dominant Dolichoderinae	Decrease
	Hot climate Specialist	Increase
Proximity to water (km)	Subordinate Camponotini	Increase
Biocrust cover (%)	Cold Climate Specialists	Increase
	Hot climate Specialists	Increase
	Subordinate Camponotini	Increase

Note. Functional group model includes environmental attributes: Shrub cover and height, grazing intensity, proximity to water, and biocrust cover.

shrubs height, consistent with our third hypothesis. *Pheidole* (Generalized Myrmicinae) declined in abundance as shrub height increased ($\chi^2_{1,32} = 2,587.6, p < .001$, Figure 4). Similarly, *Meranoplus*, a genus of Hot Climate Specialists, also declined in abundance with increasing shrub height ($\chi^2_{1,32} = 1,137.08, p < .001$).

Most functional groups showed no significant response to grazing intensity except Hot Climate Specialists, whose abundance increased with increasing grazing intensity and Dominant Dolidocherinae, which exhibited the opposite trend, thus providing mixed support for our fourth hypothesis. The increase in Hot Climate specialists was largely driven by *Meranoplus*, which increased in abundance with increasing grazing intensity ($\chi^2_{1,31} = 889.66, p < .001$). The increase in abundance of Subordinate Camponotini with increasing proximity to water was driven by the genera *Camponotus* ($\chi^2_{1,30} = 272.18, p < .001$) and *Calomyrmex* ($\chi^2_{1,30} = 13.78, p = .023$).

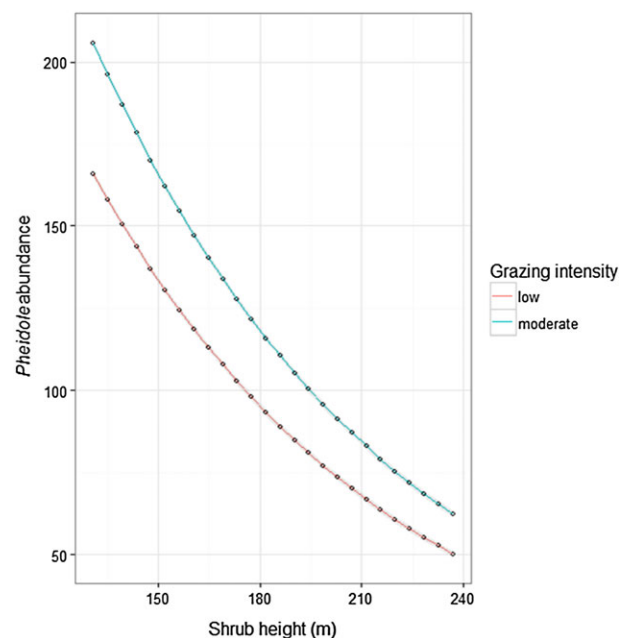


FIGURE 4 Modelled response of *Pheidole* abundance (mean $\pm 95\%$ CI) to changes in shrub height (m) and grazing intensity [Colour figure can be viewed at wileyonlinelibrary.com]

Finally, the Cold Climate Specialists, Subordinate Camponotini, and Hot Climate Specialists were more abundant at sites with larger patches of biocrust cover. This increase in Cold Climate Specialists was driven mainly by *Stigmacros* ($\chi^2_{1,29} = 54.3, p < .001$, Figure 5). Similarly, *Camponotus* (Subordinate Camponotini; $\chi^2_{1,29} = 231.49, p < .001$) and *Meranoplus* (Hot Climate Specialists; $\chi^2_{1,29} = 389.2, p < .001$) preferred sites with large patches of biocrust cover.

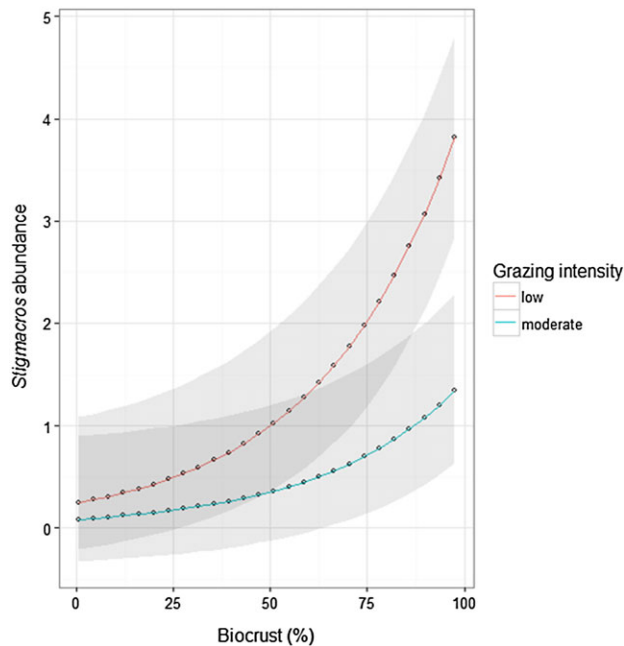


FIGURE 5 Modelled response of *Stigmacros* abundance (mean \pm 95% CI) in relation to biocrust cover (%) and grazing intensity [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Ant richness increased with increasing grazing intensity, but contrary to prediction, shrub cover (Hypothesis 1) and height had no effect on richness. Changes in grazing intensity, shrub cover and shrub height produced mixed responses in functional group composition, generally consistent with our predictions (Hypotheses 2 and 3), and functional group responses were restricted to Hot and Cold Climate Specialists, Subordinate Camponotini, Generalized Myrmicinae, and Dominant Dolichoderinae (Hypotheses 3 and 4).

4.1 | Grazing increased ant richness and altered functional group abundance

Overgrazing by livestock often leads to substantial land degradation. Higher levels of livestock grazing were associated with greater ant species richness, diversity, and evenness, and greater abundance of *Meranoplus*, a Hot Climate Specialist. However, increasing grazing intensity was associated with reduced abundance of the Dominant Dolichoderinae functional group, providing mixed support for our fourth hypothesis. The general effects of overgrazing are to reduce soil surface complexity, plant cover, and biomass and increase the area of bare soil (Vandandorj, Eldridge, Travers, & Delgado-Baquerizo, 2017). However, livestock also has indirect effects by altering competition between plant species, favouring short-lived annuals over longer-lived perennials, thereby altering the composition of the plant community (Bestelmeyer & Wiens, 2001) and thus habitat available for ants. Reductions in groundstorey plant cover, debris, and leaf litter have been shown to increase the efficiency of ant foraging because the surfaces are less complex and more homogeneous, with greater connectivity between areas of litter-free surface (Lassau & Hochuli, 2004).

Thus, these grazing-related increases in ant richness, diversity, and evenness that we observed are likely due to lower cover of vegetation associated with grazing (Seymour & Dean, 1999).

A greater area of bare soil resulting from overgrazing (Hoffmann & Andersen, 2003) might be expected to increase the likelihood of encountering predators (Wilkinson & Feener, 2012), thereby selecting for larger bodied, more aggressive ants such as the Dominant Dolichoderinae than other functional groups. Thus, the Dominant Dolichoderinae are known to be more abundant in grazed, open areas due to their competitive advantage over other ants and their ability to tolerate high surface temperatures (Lindsay & Cunningham, 2009). In our study, however, increased grazing pressure had the opposite effect and was associated with fewer Dominant Dolichoderinae. Rather, increasing grazing was associated with a greater abundance of *Meranoplus*, a Hot Climate Specialist. This is consistent with results of a study from arid South Australia where grazing increased the abundance of Hot Climate Specialists on sand dunes (Read & Andersen, 2000). The authors attributed this greater abundance to increased soil surface temperatures resulting from vegetation removal by livestock (Spence, Liancourt, Boldgiv, Petraitis, & Casper, 2014).

Livestock can also influence ant community composition by modifying habitat structure and food supply, which can alter interactions among different functional groups (Andersen, 1995). We found that abundance of Subordinate Camponotini increased, and a suggestion that abundance of Specialist Predators declined, closer to water. Our sites spanned a relatively wide gradient, extending out to distances of 5.4 km from water. Changes in abundance of these functional groups may therefore make them useful indicators of changes in grazing-induced degradation (Nash et al., 2004) and although differences were apparent very close to water, we failed to find any thresholds in abundance across the 5.4 km gradient.

4.2 | Increasing shrub cover had few effects on ants

Encroachment has been shown to increase bird (Sirami et al., 2009), mammal (Blaum et al., 2007), and invertebrate (Schirmel, Mantilla-Contreras, Gauger, & Blindow, 2015) abundance, but there have been few studies of ant responses to encroachment. Contrary to prediction (Hypothesis 1), both richness and diversity of ants were unaffected by increasing shrub cover. Indeed, previous studies have shown mixed responses of ants to changing shrub cover. For example, Wiezik et al. (2013) showed that ant richness was greatest at the site with the greatest shrub cover (41%) and attributed this to the mixture of grassland and forest species that prefer either open habitats or those with abundant leaf litter, respectively. In studies in the Chihuahuan Desert, however, abundance of the grassland seed-harvesting ant *Pogonomyrmex* declined with increasing shrub cover (Brown, Valone, & Curtin, 1997). Similarly, encroachment of mesquite (*Prosopis* spp.) into former grassland in New Mexico resulted in an increased density of the ant *Trachymyrmex smithii*, which uses mesquite leaves as a substrate for tending subterranean fungi (Eldridge, Whitford, & Duval, 2009).

The lack of a response of ant richness, diversity, and evenness to changing shrub cover reflects the idiosyncratic responses of different functional groups to changing shrub cover, with some groups increasing (Subordinate Camponotini) but most showing no response. As

predicted, the abundance of the Subordinate Camponotini group increased with increasing shrub cover. This was expected, as genera such as *Camponotus* and *Polyrhachis* are associated with shrubs and woody plants. *Camponotus* spp. use shrubs and trees for foraging and nesting (Gano & Rogers, 1983). *Polyrhachis* spp. in particular, use a wide range of habitats from subterranean to arboreal nests (Robson & Kohout, 2005). Therefore, higher levels of shrub cover would likely increase their abundance, by increasing the availability of suitable habitat and nesting material.

We did find, however, that larger shrubs tended to be associated with greater overall ant richness, greater abundance of Cold Climate Specialists, and fewer Generalized Myrmicinae and Hot Climate Specialists (Table 1), consistent with our third hypothesis. Larger woody plants are typically more structurally complex, altering microclimates (Larsson, 1989; Raghu, Drew, & Clarke, 2004), resource availability (Marques, Price, & Cobb, 2000), or predation pressures (e.g., Jeffries & Lawton, 1984). For example, a more complex shrub structure would have a greater variety of habitat resources (e.g., dead wood, bark, and leaves of different shape and size) and likely greater densities of hemipterans or leop on which ants depend (Gibb, 2012; Kwok & Eldridge, 2016). Larger more complex shrubs have been shown to be preferred habitat for Cold Climate Specialists, Cryptic Species, and Subordinate Camponotini functional groups (Hill, Summerville, & Brown, 2008). Generalized Myrmicinae and Hot Climate specialists, however, tend to forage in more open areas (Lassau & Hochuli, 2004), and the abundance of Hot Climate Specialists is known to decline in densely shaded areas associated with a well-developed leaf litter layer, such as occurs beneath shrubs (Burbidge, Leicester, McDavitt, & Majer, 1992). Thus, the reduction in abundance of Hot Climate Specialists and Generalized Myrmicinae may result from the reduction in temperature and increased habitat complexity due to high litter cover under shrubs.

Finally, our study suggests that biocrust cover was associated with a greater abundance of Cold Climate Specialists, Subordinate Camponotini, and Hot Climate Specialists. Biocrusts could increase the abundance of Cold Climate Specialists and Subordinate Camponotini during summer by providing a cooler refuge for foraging, as biocrust surfaces have lower temperatures during summer, but also higher temperatures in winter (Xiao, Wang, Fan, Fischer, & Veste, 2013). Cooler microclimates during summer are favourable for Cold Climate specialists whose distribution is centred on the cool-temperate zone (Hoffmann & Andersen, 2003) and reduced temperatures may lead to longer foraging times. They could also provide a food resource for ants and protection from predators (Li et al., 2011).

5 | CONCLUSIONS

Our study indicated that a change in grazing intensity from low to moderate levels had a greater influence on ants than changes in shrub cover from the lowest cover to the maximum cover experienced in eastern Australia. Although shrub encroachment had few effects on the ant community, we found some changes in functional group composition in response to changes in shrub height, as well as differences in relation to biocrust cover. That the effects of grazing were stronger

than shrub effects is consistent with the emerging body of literature suggesting that shrubs are not indicative of degraded systems (e.g., Eldridge & Soliveres, 2014; Maestre et al., 2016) and that putative effects of shrub encroachment can often be ascribed to overgrazing (Eldridge et al., 2013). Overgrazing, however, is a substantial cause of land degradation, and in this study, the effects of grazing on the soil surface likely lead to the changes we observed in the ant community. Although shrub cover is likely to increase globally as atmospheric CO₂ levels continue to rise, grazing is likely to have a stronger impact on ants. Any changes in ant community composition driven by overgrazing are likely to have negative impacts on drylands, influencing a wide range of ecosystem processes and services such as seed dispersal, decomposition, and nutrient cycling.

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