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Habitat-contingent responses to disturbance: impacts of cattle grazing on ant communities vary with habitat complexity

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Abstract. Predicting community responses to disturbance is a major challenge for both ecology and ecosystem management. A particularly challenging issue is that the same type and intensity of disturbance can have different impacts in different habitats. We investigate how habitat contingency influences ant community responses to disturbance in arid Australia, testing the hypothesis that disturbance has a greater impact in more complex habitats. We assess the effectiveness of a highly simplified ant assessment protocol that considers larger species only. We sampled ants at 46 sites from two habitats (Chandler, low chenopod shrubland; and mulga, low woodland) with contrasting complexity, using distance from water as a surrogate for variation in grazing intensity. We assessed variation in habitat structural variables (basal area of perennial grass, and cover of herbs, litter, and bare ground) and ant communities in relation to habitat and distance from water, first using data from the entire ant community and then for larger ants (>4 mm body length) only. Site species richness was almost twice as high in mulga, the more structurally complex habitat, than in Chandler, and ant communities in mulga showed far more variation in relation to distance from water. Litter cover was the key environmental variable associated with the interaction between grazing and habitat: it increased with increasing distance from water in mulga and was virtually absent from Chandler. Analysis of only larger species revealed the same patterns of variation in ant abundance, species richness and composition in relation to habitat and grazing as shown by entire ant communities. Our findings support the hypothesis that disturbance impacts on faunal communities increase with increasing habitat complexity. An appreciation of such habitat contingency is important for a predictive understanding and therefore effective management of disturbances such as rangeland grazing. Our findings also show that simplified assessment can provide robust information on the responses of highly diverse ant communities to disturbance, which enhances their feasibility for use as bio-indicators in land management.

Key words: ant functional groups; arid rangelands; biodiversity conservation; ecological assessment; grazing impacts; habitat contingency; rangeland management; sampling efficiency.

INTRODUCTION

Disturbance is a key factor influencing the structure and dynamics of biological communities (Sousa 1984), and predicting community responses to disturbance has been a major challenge for both ecology and ecosystem management (Bengtsson et al. 2000). The ecological impacts of disturbance vary widely depending on the type, severity, frequency and timing of disturbance (Sousa 1984, Chazdon 2003). However, a particular challenge for predicting ecological responses to disturbance is that the same type and intensity of disturbance can have different impacts in different habitats (Kaiser et al. 1998, Hansen and Clevenger 2005).

Habitat-contingent responses to disturbance can be caused by two factors. First, variation in species composition between habitats might result in variation in resilience to disturbance due to differences in the functional traits of component species (Moretti and Legg 2009, Peco et al. 2012). Second, habitats might vary in structural complexity, and therefore in the extent of structural change caused by disturbance. The same disturbance is likely to have a greater impact on the structure of complex habitats than it is on that of structurally simple habitats, resulting in stronger negative impacts of disturbance on communities in more complex habitats (Gardner et al. 1995, Broza and Izhaki 1997, Farji-Brener et al. 2002). Habitat complexity therefore not only plays a key role in directly shaping biological communities but is also an important factor influencing their responses to disturbance (McCoy and Bell 1991, Gardner et al. 1995, Hansen 2000, Tews et al. 2004). An appreciation of such habitat contingency is important for a predictive understanding and therefore effective management of disturbances impacts.

More than one-half of the world’s agricultural land surface is subjected to grazing by livestock (MEA 2005), making livestock grazing one of the major agents of disturbance globally. Grazing has a direct impact on vegetation through the removal of plant biomass, and its impacts on vegetation are often highly visible and have been extensively studied (Brathen and Oksanen 2001, Cingolani et al. 2003). However, the effects of grazing on fauna are indirect, primarily through changes in vegetation structure and associated quality and availability of resources (Kruess and Tscharntke 2002, O’Neill et al. 2003, Dennis et al. 2007). Associated faunal changes are generally not visible, have not been so extensively studied and therefore to a large extent remain
unknown. Given that faunal responses to grazing are mediated by grazing-induced vegetation change, such responses are likely to be highly habitat contingent.

Here, we investigate habitat-contingent responses of ant communities to variation in the intensity of livestock grazing in Australia’s arid rangelands. Pastoralism is the most extensive land use in Australia, occupying 58% of the country and being a particularly dominant land use in the arid and semiarid interior (ABARES 2016; Eldridge et al. 2016). Ants have frequently been used as a focal taxon for studying faunal responses to disturbance (Folgarait 1998, Hoffmann 2010, Lach et al. 2010). Ants are a ubiquitous and globally dominant faunal group, representing a large proportion of terrestrial faunal biomass (Hölldobler and Wilson 1990,) and playing many functionally important roles in ecosystems (Folgarait 1998, Del Toro et al. 2015). Combined with their ease of sampling and high sensitivity to disturbance, this makes ants ideal bio-indicators of ecosystem disturbance (Andersen and Majer 2004), and their responses to grazing have been extensively studied (Andersen et al. 2004, Hoffmann and James 2011, Moranz et al. 2013, Arcoverde et al. 2017). Habitat complexity is a major driver of ant community structure and dynamics (Andersen 1995, Gibb and Parr 2010), and a common finding of grazing studies is that ant species responses vary markedly with habitat (Hoffmann 2010).

The use of ants in ecological assessments can be time-consuming and taxonomically challenging in areas of high ant diversity (Fisher 2005, Underwood and Fisher 2006), particularly for those without specialist entomological experience. This often puts ants and other invertebrates in the “too hard” basket for land managers. A range of shortcut strategies have been used for ant assessments, including the use of genus richness as a surrogate for species richness (Andersen 1995), the use of selected target taxa (Andersen and Majer 2004), and the use of larger ant species only (Andersen et al. 2002). The latter is especially promising because large ants are especially sensitive to disturbance (Ness et al. 2004, H. Gibb et al., 2018) and are much more readily sorted to species and identified to genus than are small ants, especially by a nonspecialist. Large ants have been shown to reflect responses of overall ant communities to sulfur dioxide emissions in the Australian semiarid tropics (Andersen et al. 2002). However, the ability of large ants to reflect responses of entire communities to grazing remains unknown.

Our study examines ant responses to grazing in two land systems representing different habitat structure and complexity, using distance from water as a surrogate for variation in grazing intensity (Hoffmann 2003, Hoffmann and James 2011). We address four specific questions. First, to what extent does grazing affect habitat structure of the ground layer in the two land systems? Second, how does the taxonomic and functional composition of ant communities vary between the habitats of the two land systems? Third, to what extent are ant communities affected by grazing, and is there a significant interaction between grazing and habitat that can be explained by interactive effects on habitat structure? Finally, does analysis of only larger species reveal the same patterns of variation in relation to habitat and grazing as shown by entire ant communities?

METHODS

Study system

Our study was conducted at Henbury Station, a 5,273 km² pastoral property located 130 km south of Alice Springs in Australia’s Northern Territory. Cattle grazing was established at Henbury in 1875, and stocking rates have historically been typical (approximately 3 head/km²) for the region. Henbury Station was incorporated into Australia’s National Reserve System in 2011 and was destocked two years prior to our sampling. We note that such destocking may have resulted in lower grazing impacts at the time of our sampling. Mean annual rainfall is 220.7 mm, occurring primarily in the summer between December and April (Bureau of Meteorology 2017). The area is characterized by hot summers (mean daily temperatures ranging from 21.5°C to 36.5°C in January) and cool winters (4°C–19.7°C in July).

Henbury Station straddles the Fink and MacDonnell Ranges bioregions and includes 12 land systems, the most extensive of which are mulga country and Chandler (Fig. 1b, c; Pearse 2012). Mulga country is characterized by red earth plains supporting groves of mulga (Acacia aneura F. Muell. ex Bent.) trees up to 5 m in height, with an understory of scattered shrubs, a sparse ground layer of grasses (especially Eragrostis etiopoda Benth. Fl.) and forbs, and substantial litter and coarse woody debris, especially under canopies (Fig. 1b). The Chandler land system occurs on sandstones and shales and includes extensive clayey, stony slopes dominated by low (<1 m) chenopod shrubs dominated by Sclerolaena spp. (Perry 1962), with substantial bare ground and virtually no litter cover or coarse woody debris (Fig. 1c); we subsequently refer to this as Chandler habitat.

Ant abundance and diversity are exceptionally high in arid Australia (Andersen 2003, 2007, 2016). Communities are dominated numerically and behaviorally by species of Iridomyrmex and include numerous arid-adapted species of Melophorus, Monomorium, Camponotus, Tetramorium, Messor, and Rhytidoponera (Andersen 2003, 2007). Local ant diversity and species composition vary markedly with habitat structure and complexity (Andersen 1993, Barrow et al. 2006, Andersen and Hayward 2012). Ant diversity is especially high in mulga woodlands (Andersen and Hayward 2012), which can be explained by their provision of key resources such as honey dew and leaf litter, and by their ameliorated microclimates compared with more open, structurally simple habitats. For example, the honey pot ant Camponotus inflatus is dependent on nectar resources provided by mulga and occurs only in mulga habitat (Conway 1991). Species of the macropus group of Polyrhachis are also restricted to mulga habitats (they are colloquially known as “mulga ants”), where they incorporate mulga leaf litter into their spectacularly elaborate nest mounds, and likely also rely on mulga nectar (Andersen 2003).

Study sites

We used distance from water as a surrogate of relative grazing intensity (Hoffmann 2003, Hoffmann and James...
FIG. 1. (a) Location of the 46 study sites on Henbury Station, Australia in relation to Meteorite Dam, the only water point in the study area. Photos of (b) mulga and (c) Chandler land systems on Henbury Station. In panel c, mulga can be seen in the background.
ANTS RESPONSES TO GRAZING

October 2018

Cattle need to drink each day, and grazing intensity is highest very close to water, and decreases in radial symmetry with increasing distance out to about 8 km, with relatively low levels of grazing beyond 3 km (Foran 1980, Ludwig et al. 1999). We surveyed ants at 46 sites (16 mulga and 30 Chandler) at distances out to 6 km from a permanent water point (Fig. 1a). Mulga habitat was restricted to the western side of the water point, and so only a single transect was possible; Chandler was sampled using two orthogonal transects from the water point (Fig. 1a). Mulga sites varied from 0.8 to 6 km from the water point, and Chandler from 0.03 to 6 km. Sites were separated by a minimum of 100 m.

Ant sampling, identification, and classification

Ants were sampled using 45 mm diameter pitfall traps (plastic specimen containers, partly filled with ethylene glycol as a preservative). A 4 × 5 grid of traps with 10 m spacing was established at each site and operated for a 48-h period in September 2013.

Ants were sorted to species, and where possible named based on comparisons with specimens held in the CSIRO Tropical Ecosystems Research Centre, Darwin. Most of the species could not be named and were identified to genus and species group following Andersen (2000), and species within a genus were assigned code numbers (e.g., sp. A) unique to this study. Voucher specimens of all species are deposited in the CSIRO Tropical Ecosystem Research Centre. We recorded the abundance of each species in each pitfall trap, capped at 100 individuals per species per trap to avoid possible data distortions resulting from very high numbers of individuals from the same colony falling into one or a few traps (Andersen 1991).

Ant species were classified into one of six functional groups in relation to environmental stress and disturbance, based on Andersen (1995): dominant Dolichoderine, generalized Myrmicinae, opportunists, subordinate Camponotini, hot-climate specialists, and specialist predators.

We followed Andersen et al. (2002) in using body length >4 mm as a guide to selecting larger ants. We defined larger ants as all species within the genera Lioponera, Rhytidoponera, Anochetus, Odontomachus, Leptogenys, Camponotus, Calomyrmex, Polyrhachis, and Opisthopsis, as well as species of the impressum and spininode groups of Tetramorium, bagoti group of Melophorus, whitei complex of Monomorium, and the purpureus, agilis, and roseatus groups of Iridomyrmex.

Ground layer habitat structure

To assess the impact of cattle grazing on ground layer habitat structure, we used 1 × 1 m quadrats centered on each pitfall trap (i.e., 20 quadrats per site) to estimate the basal area of perennial grass, and the percent cover of herbs (annual grasses and forbs), litter, gravel, and bare ground.

Analysis

We used multiple linear regression to analyze variation in each environmental variable in relation to distance from water to habitat. Analyses were performed using the multcomp package in R (R Core Team 2015).

We used general linear models (GLM) to analyze variation in ant abundance and species richness in relation to habitat, distance from water, and measured environmental variables. We used Poisson error distribution for species richness and quasi-Poisson error distribution for abundance to account for over-dispersed data (Crawley 2007). We repeated this analysis considering larger species only. We also conducted GLM on the abundance of the most common individual species, defined as those occurring at >15 sites and with >300 total individuals. We repeated this analysis for the abundance of each functional group, using Poisson and quasi-Poisson error distributions when necessary to account for over-dispersed data. Models were checked for outliers, overly influential observations, homoscedasticity, and normal distribution of residuals. Analyses were performed using the car package in R (R Core Team 2015).

We used canonical correspondence analyses (Ter Braak 1986) to evaluate variation among sites in ant species and functional group composition, and how such variation was associated with distance from water, habitat and environmental variables. We conducted randomization tests (10,000 randomizations) to check the statistical significance of habitat and distance from water as predictor variables, along with their interaction (Legendre et al. 2011). We repeated these analyses for the larger species only. The analyses were performed using the vegan package in R (R Core Team 2015).

RESULTS

We recorded a total of 25,205 ants from 136 species and 17 genera. The richest genera were Melophorus (32 species), Iridomyrmex (29), Monomorium (19), and Tetramorium (18). The most common species were Iridomyrmex chasiei (representing 26.7% of all ants, present in 69% of the plots), Iridomyrmex sp. R1 (rufoniger gp.; 21.5%, 59%), and Monomorium subapterum (15.1%, 98%), which together represented 63.3% of all ants collected. Considering only larger species, we recorded a total of 2,069 ants from 28 species and 13 genera. The richest genera were Rhytidoponera (5 species), Camponotus (5), and Iridomyrmex (4), and the most common species were Iridomyrmex viridiaeus (representing 23.9% of all larger ants, present in 30.6% of the plots), Rhytidoponera sp. C (reticulata gp.; 19.1%, 30.6%), Tetramorium sp. A (impressum gp.; 15.9%, 30.6%), Iridomyrmex agilis (10.8%, 24.5%), and I. roseatus (8.3%, 20.4%), which together represented 78% of all larger ants collected.

Ground layer habitat structure

All environmental variables varied significantly with habitat, distance from water or their interaction, except for basal area of perennial grass (which averaged about 11% throughout; Table 1). The percent cover of bare ground (Chandler, 32 ± 2.7; mulga, 53.3 ± 2.2) and gravel (Chandler, 37.1 ± 2.7; mulga, 0.0) varied only with habitat (Table 1). Litter cover varied with habitat (litter was virtually absent from Chandler sites) and was the only measured
Table 1. Summary of multiple linear regression of the five environmental variables and summary of GLM results of the nine most common species (of 13) and functional groups (considering all ant species) in relation to the impact of distance from water (Dist), habitat, and their interaction (Dist × Habitat).

<table>
<thead>
<tr>
<th>Response variable and factor</th>
<th>Sum of squares</th>
<th>F</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Perennial grass basal area</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dist</td>
<td>11.3</td>
<td>0.398</td>
<td>1</td>
<td>0.531</td>
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<tr>
<td>Habitat</td>
<td>2.5</td>
<td>0.087</td>
<td>1</td>
<td>0.769</td>
</tr>
<tr>
<td>Dist × Habitat</td>
<td>3.4</td>
<td>0.121</td>
<td>1</td>
<td>0.729</td>
</tr>
<tr>
<td><strong>Bare ground</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dist</td>
<td>271</td>
<td>1.61</td>
<td>1</td>
<td>0.212</td>
</tr>
<tr>
<td>Habitat</td>
<td>4721</td>
<td>28.1</td>
<td>1</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td>Dist × Habitat</td>
<td>41</td>
<td>0.243</td>
<td>1</td>
<td>0.624</td>
</tr>
<tr>
<td><strong>Gravel</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dist</td>
<td>1</td>
<td>0.007</td>
<td>1</td>
<td>0.93</td>
</tr>
<tr>
<td>Habitat</td>
<td>14331</td>
<td>95.61</td>
<td>1</td>
<td>&lt;0.001*</td>
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<tr>
<td>Dist × Habitat</td>
<td>0</td>
<td>0.001</td>
<td>1</td>
<td>0.97</td>
</tr>
<tr>
<td><strong>Litter</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dist</td>
<td>25.4</td>
<td>2.36</td>
<td>1</td>
<td>0.13</td>
</tr>
<tr>
<td>Habitat</td>
<td>2208.9</td>
<td>205.1</td>
<td>1</td>
<td>&lt;0.001*</td>
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<tr>
<td>Dist × Habitat</td>
<td>88.6</td>
<td>8.23</td>
<td>1</td>
<td>0.006*</td>
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<tr>
<td><strong>Herbs</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dist</td>
<td>163.5</td>
<td>9.89</td>
<td>1</td>
<td>0.003*</td>
</tr>
<tr>
<td>Habitat</td>
<td>207</td>
<td>12.52</td>
<td>1</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td>Dist × Habitat</td>
<td>8.8</td>
<td>0.53</td>
<td>1</td>
<td>0.47</td>
</tr>
<tr>
<td><strong>Iridomyrmex chasei</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Dist</td>
<td>0.851</td>
<td>44</td>
<td>0.361</td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td>6.033</td>
<td>43</td>
<td>0.018*</td>
<td></td>
</tr>
<tr>
<td><strong>Iridomyrmex sp. R1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Dist</td>
<td>0.01</td>
<td>44</td>
<td>0.919</td>
<td></td>
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<tr>
<td>Habitat</td>
<td>15.23</td>
<td>43</td>
<td>&lt;0.001*</td>
<td></td>
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<tr>
<td><strong>Iridomyrmex viridians</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dist</td>
<td>1.45</td>
<td>44</td>
<td>0.235</td>
<td></td>
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<tr>
<td>Habitat</td>
<td>3.02</td>
<td>43</td>
<td>0.09</td>
<td></td>
</tr>
<tr>
<td><strong>Melophorus sp. W1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dist</td>
<td>30.18</td>
<td>43</td>
<td>&lt;0.001*</td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td>9.55</td>
<td>44</td>
<td>0.003*</td>
<td></td>
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<tr>
<td><strong>Melophorus sp. T1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dist</td>
<td>1.82</td>
<td>44</td>
<td>0.185</td>
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<tr>
<td>Habitat</td>
<td>33.288</td>
<td>43</td>
<td>&lt;0.001*</td>
<td></td>
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<tr>
<td><strong>Melophorus sp. F4</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Dist</td>
<td>3.09</td>
<td>44</td>
<td>0.086</td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td>30.82</td>
<td>43</td>
<td>&lt;0.001*</td>
<td></td>
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<tr>
<td><strong>Melophorus sp. P1</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Dist</td>
<td>0.014</td>
<td>44</td>
<td>0.905</td>
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<tr>
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<td>22.52</td>
<td>43</td>
<td>&lt;0.001*</td>
<td></td>
</tr>
<tr>
<td><strong>Melophorus sp. F2</strong></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Dist</td>
<td>75.94</td>
<td>43</td>
<td>&lt;0.001*</td>
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<tr>
<td>Habitat</td>
<td>12.22</td>
<td>44</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td><strong>Melophorus sp W4</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Dist</td>
<td>2.522</td>
<td>43</td>
<td>0.12</td>
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<tr>
<td>Habitat</td>
<td>0.01</td>
<td>44</td>
<td>0.918</td>
<td></td>
</tr>
<tr>
<td><strong>Tetramorium sp. A</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dist</td>
<td>54.08</td>
<td>43</td>
<td>&lt;0.001*</td>
<td></td>
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<tr>
<td>Habitat</td>
<td>5.83</td>
<td>44</td>
<td>0.02*</td>
<td></td>
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<tr>
<td><strong>Monomorium sp. S1</strong></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Dist</td>
<td>0.207</td>
<td>43</td>
<td>0.651</td>
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<tr>
<td>Habitat</td>
<td>0.853</td>
<td>44</td>
<td>0.361</td>
<td></td>
</tr>
<tr>
<td><strong>Rhytidoponera sp. C</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dist</td>
<td>0.064</td>
<td>43</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td>2.332</td>
<td>44</td>
<td>0.134</td>
<td></td>
</tr>
</tbody>
</table>

Note: *P < 0.05, LA, large ants.

Ant abundance and richness

Overall ant abundance did not vary with habitat or distance from water, considering either all species (493 ± 93.5 cf. 651 ± 65.3; F_{1,44} = 0.53, P = 0.47 and F_{1,43} = 1.79, P = 0.18, respectively) or large ants only (37.5 ± 9 cf. 61.6 ± 19; F_{1,43} = 0.21, P = 0.64 and F_{1,42} = 2.9, P = 0.09, respectively). Mean ant richness was far higher at mulga than Chandler sites, for both the whole community (25.8 ± 0.9 cf. 19.5 ± 2.9) and large ants only (3.1 ± 0.6 cf. 2.9 ± 0.6). Mean species richness did not vary with distance from water for either the whole community (X^2_{1,43} = 1.23, P = 0.27) or for large ants only (X^2_{1,42} = 0.83, P = 0.35). The abundances of eight of the 13 most common species showed significant variation in relation to habitat (see Appendix S1: Fig. S1; Table 1): *Melophorus sp. W1, Iridomyrmex chasei, Melophorus sp. P1, Melophorus sp. T1, Melophorus sp. F4, Tetramorium sp. A, Monomorium sp. S1, Rhytidoponera sp. C.*
and *Tetramorium* sp. A were more abundant at Chandler sites, whereas *Iridomyrmex* sp. R1, *Melophorus* sp. T1, *Melophorus* sp. F4, and *Melophorus* sp. R2 were more abundant in mulga. The abundances of none of the four species occurring most commonly at Chandler sites varied in relation to distance from water. In contrast, the abundances of three species occurring most commonly in mulga varied with distance from water (*Melophorus* sp. F2 and *Tetramorium* sp. A) increased in abundance with increasing distance, and *Melophorus* sp. W1 decreased. Appendix S1: Fig. S1), and the abundance of the fourth, *Iridomyrmex* sp. R1, increased with increasing litter cover (*F*1,42 = 6.7, *P* = 0.013; see Appendix S1: Fig. S1).

The abundances of two functional groups varied significantly between the two habitats: hot-climate specialists and subordinate Camponotini were both more abundant in mulga, when considering either all ants or larger species only (see Appendix S1: Fig. S2; Table 1). Specialist predators were the only functional group varying in abundance with distance from water, increasing with increasing distance (see Appendix S1: Fig. S2; Table 1).

**Species composition**

Species composition of the entire ant community (Fig. 3a) varied with habitat (*χ*2 = 0.3763, *F*1,42 = 4.582, df = 1, *P* = 0.001), distance from water (*χ*2 = 0.1335, *F*1,41 = 1.6255, df = 1, *P* = 0.201), and litter cover (*χ*2 = 0.1232, *F*1,40 = 1.499, df = 1, *P* = 0.444). There was a significant interaction between habitat and distance from water, with mulga sites showing far greater variation in relation to distance from water than did Chandler sites (Fig. 3a). The composition of larger ant species (Fig. 3b) varied with distance from water (*χ*2 = 0.1634, *F*1,41 = 2.0232, df = 1, *P* = 0.05), habitat (*χ*2 = 0.469, *F*1,40 = 5.755, df = 1, *P* = 0.001), and their interaction, with mulga sites also showing far greater variation in relation to distance from water than did Chandler sites (Fig. 3b).

Considering all ants, functional group composition did not vary with either distance from water (*χ*2 = 0.009, *F*1,42 = 1.88, df = 1, *P* = 0.129) or habitat (*χ*2 = 0.009, *F*1,41 = 1.896, df = 1, *P* = 0.123). In contrast, functional group composition of larger ants varied with both distance from water (*χ*2 = 0.067, *F*1,41 = 4.2014, df = 1, *P* = 0.017) and habitat (*χ*2 = 0.083, *F*1,40 = 5.1430, df = 1, *P* = 0.005).

**Discussion**

Our study investigated the extent to which ant responses to cattle grazing are habitat-contingent, with the hypothesis that grazing has a greater impact in structurally more complex habitats. We also examined the extent to which analysis of only larger species reveals the responses of entire ant communities, in the context of increasing the efficiency and tractability of using ants as indicators of ecological change. Our findings support the hypothesis that grazing has a higher impact in more complex habitat and show that responses of larger ants provide a reliable representation of those of entire ant communities.

Our first aim was to examine the extent to which grazing affected habitat structure of the ground layer in the two habitats. Almost all the measured environmental variables varied with habitat, but only the cover of litter (which was virtually absent from Chandler sites) and herbs varied with distance from water and therefore grazing intensity. Both variables decreased with increasing grazing, which is typically the case in Australian rangelands (Eldridge et al. 2016) and those elsewhere (Naeth et al. 1991, Luo et al. 2010). The effect on litter was presumably due to trampling rather than consumption, whereas the effect on herbs is more likely to reflect consumption, but possibly also soil compaction. The lack of response of perennial grasses to grazing reflects a combination of high resilience of grass basal area (Coughenour 1985) and two years of recovery following destocking.

Our second aim was to examine the extent to which taxonomic and functional composition of ant communities vary between the different habitats of the two land systems. Mean site richness was nearly twice as high at mulga as Chandler sites. This is consistent with the general finding that ant diversity is markedly higher on sandy soils, such as those of mulga sites, than on clay soils, such as those of Chandler (Andersen et al. 2015, Arcovore et al. 2017, Oliveira et al. 2017). However, it can also be partly attributable to the higher habitat complexity of mulga, and particularly its dominance by trees. For example, the richness of Subordinate Camponotini (mostly species of *Camponotus*) was substantially higher at mulga (seven species) than Chandler (two species) sites, which can be directly attributable to trees,
given that many of the species forage arboreally for honeydew and extra-floral nectar (Andersen 1995).

Our third aim was to investigate the extent to which ant communities are affected by grazing, and if there is a significant interaction between grazing and habitat that can be explained by interactive effects on habitat structure. We found no effect of grazing on overall ant abundance or species richness, but a substantial impact on taxonomic and functional composition. This is consistent with the general finding that the composition of ant communities is far more sensitive to grazing than is overall ant abundance or species richness (Hoffmann 2010). Changes in ant composition but not richness reflects winner–loser replacement, where species that are sensitive to disturbance (losers) are replaced by species that benefit from it (Andersen 1997, Hoffmann and Andersen 2003, Leal et al. 2012, Oliveira et al. 2017).

Of the most common species, we identified Melophorus sp. W1 as a grazing winner and Tetramorium sp. A and Melophorus sp. F2 as grazing losers.

We found a significant interaction between grazing and habitat that could be attributed to differences in habitat complexity. Grazing had a greater impact on ant species and functional composition at mulga than Chandler sites, which is consistent with the higher structural complexity of mulga compared with Chandler vegetation. In particular, litter cover at mulga sites was reduced from about 20% to 5% under high levels of grazing, whereas litter was virtually absent from all Chandler sites. Litter cover is known to be a major factor influencing ant communities (Majer et al. 1984, Andersen 1995, Kaspari and Weiser 1999, Lassau and Hochuli 2004). More generally, our findings are consistent with those of other studies that have shown ant communities from more complex habitats to be more sensitive to disturbance (Farji-Brener et al. 2002, Parr et al. 2004, Barrow et al. 2007), as is the case for other arthropod groups (Gardner et al. 1995, Broza and Izhaki 1997). A recent review of grazing impacts in Australia found that responses to grazing vary between ecoregions (Eldridge et al. 2016), and we suggest that this might reflect variation in habitat complexity.

Our final aim was to assess if analysis of only larger species reveals the same patterns of variation in relation to habitat and grazing as shown by entire ant communities. We found this generally to be the case, with similar results for ant abundance, species richness and composition. The one exception was for functional composition: analysis of the entire community showed no significant variation, whereas analysis of only larger species showed significant variation in relation to grazing, land system, and their interaction. Notably, analysis of only larger species found dominant Dolichoderinae and specialist predators to be increasers and

![Graphs showing canonical correspondence analysis of ant species composition and functional group composition considering all species, and larger species only at Henbury Station.](image)

**Fig. 3.** Canonical correspondence analysis of ant species composition considering (a) all species and (b) larger species only, and ant functional group composition considering (c) all community and (d) larger ants only at the 46 study plots in Henbury Station. Variation in species composition was related to habitat, distance from water to herb cover (shown by vectors). Variation in functional group composition of entire community was related to herb cover and litter while variation of larger ants was related to distance from water, habitat, and herb cover (shown by vectors). Circles represent Chandler sites and squares represent mulga sites, distance from water is represented by colors where darker symbols are closer to water and open symbols further from water.
decreasers, respectively, in relation to increasing grazing pressure. Dominant Dolichoderinae are more generally disturbance increasers because of their strong preferences for open habitats (Hoffmann and Andersen 2003), and specialist predators are especially sensitive to disturbance globally (Hoffmann and Andersen 2003, Leal et al. 2012, Solar et al. 2016). This suggests that restricting analysis to larger species might even provide a more sensitive measure of ant responses to grazing than does analysis of entire communities, which reflects a higher sensitivity of large ants to disturbance (Ness et al. 2004; H. Gibb et al., 2018). We acknowledge that areas of low ant diversity are likely to have insufficient numbers of large species to restrict analysis to them. However, when overall ant diversity is low the overall fauna can be readily assessed without a need for simplification.

In conclusion, our work supports the habitat-contingent nature of responses of biological communities to disturbance, and in particular, the hypothesis that disturbance impacts is greater in habitats of higher complexity. An appreciation of such habitat contingency is important for a predictive understanding of disturbance impacts, and therefore for their effective management. Our findings also show that simplified assessment targeting larger species can provide robust information on the responses of a dominant invertebrate group to disturbance. This makes the use of invertebrates as bio-indicators in land management a far more tractable proposition.

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SUPPORTING INFORMATION
Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1770/full

DATA AVAILABILITY
Data available from the Charles Darwin University's eSpace Institutional Repository: https://doi.org/10.4225/37/5b0cb03d6d5c5