

# Soil surface complexity has a larger effect on food exploitation by ants than a change from grassland to shrubland

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**Abstract.** 1. Changes in vegetation community composition, such as a transition from grassland to shrubland (woody encroachment), are associated with reductions in plant cover and increases in bare ground. Encroachment-driven changes in surface cover at small spatial scales can alter ant community assemblages by changing their foraging behaviour and their ability to locate and monopolise resources.

2. Artificial arenas with three levels of complexity were used to examine changes in ant foraging efficiency, body size and ability to monopolise food. The three levels of complexity included a control (no substrate), low-complexity treatment (woody debris) and high-complexity treatment (leaf litter).

3. No difference was found in ant species composition within the complexity arenas between grassland and shrubland, but ant functional groups ‘generalised Myrmicinae’ and ‘subordinate Camponotini’ were more abundant in grassland arenas, whereas ‘opportunists’ were more abundant in shrubland arenas. Ants took twice as long to find baits in high-complexity treatments, and 1.5 times as long in low-complexity treatments, than in control treatments, which were bare arenas with no substrate. Ant body size declined with increasing surface complexity, suggesting that larger ants are discouraged from foraging in complex habitats.

4. There was also significantly greater monopolisation of the protein bait (tuna) in low- and high-complexity treatments, but there were no differences between tuna and carbohydrate (honey) in the control treatment. Consistently, no differences were found in ant behaviour between grasslands and shrublands.

5. The present study shows that ants are more responsive to small-scale alterations in soil surface complexity than to changes in vegetation community composition. Changes in soil surface complexity select for ants based on body size, which in turn influences their foraging success. Changes in vegetation complexity at small spatial scales are therefore likely to influence ant behaviour and abundance of some functional groups, potentially having an effect on the many ecosystem functions carried out by ants.

**Key words.** shrub encroachment, woodlands, foraging, bait discovery, foraging efficiency, body size index, monopolisation.

## Introduction

Shrub encroachment is a worldwide phenomenon that occurs in a range of habitats from deserts (Bestelmeyer, 2005) to alpine ecosystems (Brandt *et al.*, 2013). Encroachment is characterised by an increase in the cover and/or density of native

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shrubs at the expense of herbaceous understorey plants (Van Auken, 2009) and often changes in the vertical structure of the original grassland community (Sirami *et al.*, 2009). Alterations to vegetation structure lead to changes in landscape- and habitat-level complexity and above-ground productivity for grass- or shrub-dependent organisms. Above-ground productivity may be more spatially variable in shrublands than in the original grassland from which they are derived (Huenneke *et al.*, 2002) because shrub encroachment is often associated with large patches of bare soil, particularly where sites are overgrazed (Eldridge & Soliveres, 2015; Eldridge *et al.*, 2015). These changes in ecosystem structure can alter the abiotic and biotic environments of the original grassland by increasing leaf litter beneath shrub canopies (Maestre *et al.*, 2009; Tighe *et al.*, 2009) and reducing the abundance and richness of perennial grasses (Barbosa da Silva *et al.*, 2016). Shrub encroachment can alter the abiotic environment by increasing surface temperatures in the interspaces, and change water infiltration and the availability of carbon and nitrogen (Schlesinger *et al.*, 1990; Eldridge *et al.*, 2011).

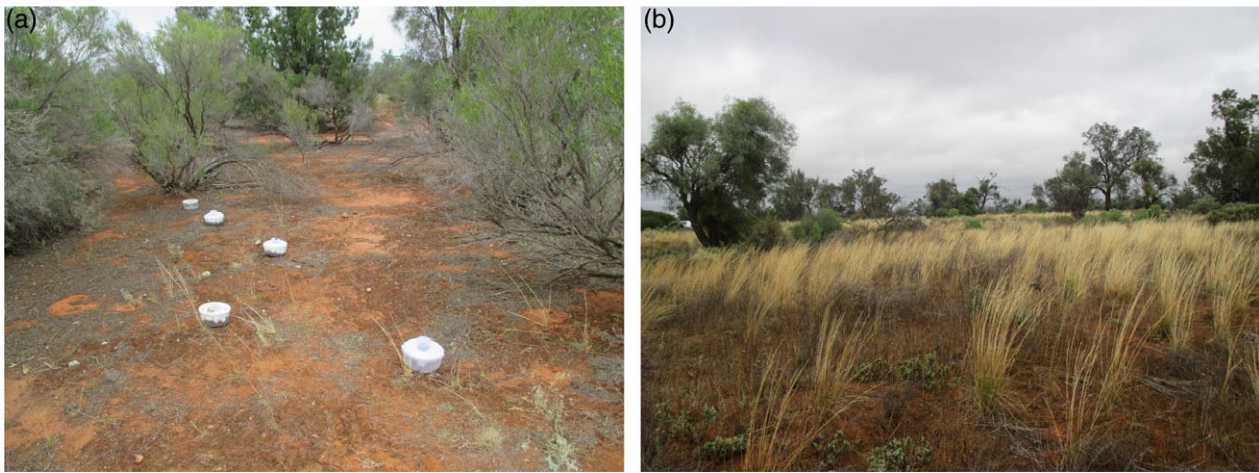
Shifts in environment complexity associated with shrub encroachment have been shown to have marked effects on birds (Sirami & Monadjem, 2012) and mammals (Blaum *et al.*, 2007), as well as invertebrates such as ants (Wiezik *et al.*, 2013). Previous studies have shown that ant abundance increases with shrub encroachment but that species richness is either unaffected by encroachment or greater in areas with low levels of shrub encroachment (Bestelmeyer, 2005; Blaum *et al.*, 2009; Dahms *et al.*, 2010). Similarly, ant composition has been shown to change over shrub encroachment gradients (Wiezik *et al.*, 2013). High levels of encroachment may increase ant populations by increasing available nesting sites or the availability of specific food resources such as carbohydrate-rich exudates from hemipteran insects (Bestelmeyer, 2005). Low levels of encroachment may enhance ant diversity and alter ant composition by allowing woodland and forest specialists to coexist with grassland species (Wiezik *et al.*, 2013).

Although we know that ant abundance, richness and composition can be affected by shrub encroachment, we know very little about how changes in ant assemblages from the original grassland affect ant activity and interspecific interactions. In particular, few studies have examined how different ant assemblages in grasslands and shrublands respond to changes in soil surface complexity, and whether this influences ant foraging efficiency, body size, and ability to monopolise food resources. Ants have relatively low dispersal capabilities compared with mammals and birds, and are known to be sensitive to disturbances (Hoffmann & Andersen, 2003; Andersen *et al.*, 2004). Similarly, ants can be highly abundant and usually comprise a range of trophic specialists such as detritivores, herbivores, and predators (Kaspari *et al.*, 2000). For these reasons, they have been used as bioindicator species to monitor the impacts of disturbances such as grazing, fire, mining, and logging (Read & Andersen, 2000; Andersen *et al.*, 2004; Hoffmann, 2010). Additionally, ants provide a number of key ecosystem services such as water infiltration, nutrient cycling (Lobry de Bruyn, 1999; Chen & Li, 2012), and seed dispersal (Servigne & Detrain, 2008). It is important, therefore, to understand how ant activity and

foraging behaviour change within the different strata between shrub-encroached environments and grasslands, as substantial changes in ant activity within these strata may affect ecosystem functionality.

Soil surface complexity shapes ant communities by influencing ant mobility and thus foraging efficiency, interspecific competition for common food resources, and the likelihood of encountering predators (Wilkinson & Feener, 2012). Complex surface environments, such as those with high levels of leaf litter, are known to increase ant foraging time and reduce efficiency as locomotion is hindered over uneven surfaces (Crist & Wiens, 1994). This is particularly obvious in large-bodied species (Gibb & Parr, 2010). Ants generally prefer to forage in simple environments as it is easier to locate and remove resources (e.g. Fewell, 1988a). Furthermore, complex environments increase the number of resources available and allow for niche differentiation (Retana & Cerdá, 2000), therefore reducing interspecific competition. This allows submissive species to coexist with dominant species as resources are harder to protect and there are fewer interactions between submissive and dominant species (Sarty *et al.*, 2006). For example, Australia's dominant genus *Iridomyrmex* is known to suppress ant richness in simple open environments (Andersen & Patel, 1994) as its ants outcompete submissive species for food resources (Gibb, 2005). Finally, ant body size declines with increasing complexity (Farji-Brener *et al.*, 2004). Large ant species with long legs perceive their environment as more planar (Sarty *et al.*, 2006) and are able to travel and forage across leaf litter, whereas small-bodied ants with short legs perceive their environment as more rugose and are more successful foraging through leaf litter (Wiescher *et al.*, 2012). Thus larger-bodied and long-legged ant species are more effective at foraging in planar environments, whereas their small-bodied counterparts are more effective at foraging within complex environments such as leaf litter (Gibb & Parr, 2010).

We used an experimental approach, with artificial arenas, to examine how changes in soil surface complexity affected ant richness, functional group composition, and ant activity in two markedly different vegetation communities. We expected that the effects of complexity on ant foraging efficiency would differ between the two communities that support different ant assemblages. We conducted our study in shrubland and grassland vegetation communities because these communities are markedly different in structure, have different soil surface characteristics, and generally support different ant assemblages. We expected that shrublands would support a greater abundance of aggressive and dominant ant species (dominant Dolichoderinae) because they prefer hot and open environments (Andersen, 1995) as well as arboreal species such as *Camponotus*, a genus of the functional group subordinate Camponotini (Bestelmeyer & Schooley, 1999). Conversely, we predicted that grasslands would support cold climate specialists, which are more abundant in habitats with a low abundance of dominant Dolichoderinae ants (Hoffmann & Andersen, 2003). Within the complexity arenas, we predicted that ants would detect food resources more rapidly in simple than in complex environments, because complex environments hinder mobility (Crist & Wiens, 1994). Second, we predicted that body size would decline with increasing complexity as small ants are more efficient at foraging within



**Fig. 1.** Images of shrubland (a) and grassland (b) near Mildura in eastern Australia. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

complex environments (Gibb & Parr, 2010) where resources are often found within the litter itself. Finally, we predicted that higher monopolisation of food baits would occur in more simple habitats such as shrubland because resources would be easier to find and defend in large bare soil interspaces, particularly for dominant ant species (Retana & Cerdá, 2000), which are known to displace submissive species.

## Methods

### Study sites

To assess how vegetation community and surface complexity affect ant communities, we used six grassland and six shrubland sites close to the city of Mildura, Australia (34° 15'S, 142° 4'E). Average rainfall for Mildura over the past decade has ranged from 123.2 to 657.4 mm (BOM, 2017). Summer temperatures ranged from a minimum of 16.9 °C to a maximum of 33.1 °C, and winter temperatures from 4.5 to 15.8 °C (BOM, 2017). Soils at the sites are calcareous earths with gradational profiles and surface textures ranging from sandy loams to clay loams, moderately alkaline (pH 7.5–9.0), and with low levels of soil carbon and nitrogen (Nash *et al.*, 2011). The vegetation is classified as semi-arid woodland and is dominated by the trees *Casuarina cristata* and *Eucalyptus* spp., with the intervening areas between trees dominated by shrubs (Fig 1a; 'shrublands') or grasses (Fig. 1b; 'grasslands'). Shrublands comprised the shrub species *Acacia* spp., *Grevillea* spp., *Atriplex* spp., and *Dodonaea viscosa*, with a mixed understorey grass layer. Maximum shrub height was 2.5 m and the soil surface consisted of large bare interspaces between individual shrubs but with accumulations of leaf litter under the shrub canopy and around woody debris (Daryanto & Eldridge, 2012). Grasslands had a mixed understorey grass layer with scattered shrubs and trees. Annual and perennial grasses were up to 1.1 m tall and grasses were uniformly spaced 20–30 cm apart. Tree cover averaged 35% in woodlands and < 5% in grasslands. Shrub cover is highly variable, with maximum cover up to about 40% in shrublands and

smaller patches in grasslands (Eldridge *et al.*, 2013). At the time of the study, groundstorey cover averaged about 20% cover in the woodland and 10% in the grassland.

### Experimental design and habitat complexity treatments

In January 2015 we conducted a field-based experiment at 12 randomly located sites, six in grasslands and six in shrublands, to examine the effects of plant community and habitat complexity on aspects of foraging by ants (Figure S1). The 12 sites were separated by distances of more than 2 km, and represented discrete and independent patches of vegetation. Within each site we selected three blocks that were separated by at least 100 m. Thus we had a total of 36 blocks, which formed the basis of our experimental design.

Within each block we placed six experimental arenas (sensu Gibb & Parr, 2010) to assess how habitat complexity affects ant foraging efficiency, body size, and monopolisation (Fig. S1). Experimental arenas were round, transparent, plastic containers (diameter 18 cm, height 9 cm; Fig. S2). The six arenas within a block were separated by distances of 1–3 m and represented three levels of complexity (control, low, or high complexity) and two levels of bait (honey, tuna). We used honey (carbohydrate) and tuna (protein) baits as proxies for naturally occurring plant sugars, such as those from extrafloral nectaries and honeydew excreted from hemipterans, and protein-rich sources, such as invertebrate prey, respectively. We chose to use artificial resources rather than naturally occurring sources in order to maintain consistency in food fragment size between complexity treatments and sites. We wanted to use two different bait types in order to attract a greater diversity of ant dietary groups, which included omnivorous, carnivorous, and sugar feeding species. This allowed us to determine which ground-dwelling diurnal ant species were active within the grassland and shrubland habitats, and provided insights into whether the foraging behaviour of these species differed between the soil surface strata. We acknowledge, however, that tuna is a rich protein source and is

likely to have attracted many more ant species than under natural conditions with natural baits.

Baits were placed in the centre of each arena in an observation chamber in the centre of the plastic container that allowed the observer to observe ants entering the arena and interacting with the baits. Ants were able to access food baits through 24 circular openings, 1 cm in diameter, around the circumference of the arena, and through eight 1 cm circular openings at the base of the observation chamber. Thus, in total, there were 216 arenas: two communities  $\times$  six replicates of community  $\times$  three blocks  $\times$  three complexity levels  $\times$  two bait types.

To create arenas of different complexity, we added different substrate, such as leaf litter and woody debris, from each site to the space between the arena wall and the observation chamber (Fig. S2). The control treatment had no substrate present, the low-complexity treatment consisted of twigs and sticks, and the high-complexity treatment of dense leaf litter. To maintain consistency between the low- and high-complexity treatments at different sites, we used a similar number of leaves and twigs. A layer of cotton wool was placed on top of the substrate in the low- and high-complexity treatments to force ants to walk through the substrate rather than over it to access food baits. By using a closed arena, we were able to examine whether activity changed within the different strata between shrublands and grasslands from planar microhabitats that represent bare soil patches (control treatment) to rugose microhabitats such as leaf litter (high-complexity treatment), which occur naturally in these two vegetation communities. Prior to the experiment, differences in gap size between the low- and high-complexity treatments were measured. To do this we placed the arenas over a light source and traced the gaps (exposed light) onto transparent paper where the height and width were measured to the nearest 1 mm and averaged over each individual arena. Gap height (mean  $\pm$  SE;  $11.2 \pm 1.7$  mm) and width ( $14.7 \pm 2.4$  mm) were greater in size and more variable within the low-complexity than in the high-complexity (height  $3.8 \pm 0.6$  mm, width  $4.4 \pm 0.53$  mm) treatments.

The experimental arenas prevented ants from taking a 'short-cut' to the baits. Therefore, all ants, regardless of body size, had to negotiate a route through the litter to access the baits. This could be seen to be somewhat artificial and unrepresentative of natural conditions. However, in these environments, most of the resources would be found beneath the litter, so it is reasonable that ants should make their way through the litter to access these resources. If one of the effects of shrub encroachment is to alter surface complexity by creating larger, litter-free patches or less complex litter, then larger ants could potentially be advantaged by being able to reach and monopolise resources more quickly. Conversely, smaller ants would probably have a greater advantage over larger ants in environments with deeper, more complex litter.

We observed ants over a 10-h period split into morning (08.00–11.00 hours) and afternoon (15.00–18.00 hours) sessions to sample times of similar temperature for optimum ant activity. To measure the discovery time, arenas were observed on a 2-min rotation to measure the time taken for ants to interact with baits. Ants that discovered the baits and interacted

with food were collected from the observation chamber with tweezers to assess differences in ant species between the two communities. We then recorded the number of species and the number of individual workers per species that were interacting with baits three times during the morning session (09.00, 10.00, and 11.00 hours) and three times during the afternoon session (16.00, 17.00, and 18.00 hours). Similar to the data collection for bait discovery time, we used a 2-min rotation between arenas and up to six individuals of each species were collected, using the same technique, for identification. Although we were able to derive information on abundance, richness, and composition of ants from all sites, values reported in this manuscript are based on captures at the arenas only, and are therefore not indicative of community-level values.

We assessed the cover of bare soil, litter, biocrusts (assemblages of lichens, bryophytes, and cyanobacteria on the soil surface), and herbaceous plants using a 1-m<sup>2</sup> quadrat divided into 100 sections. Within the same quadrat we measured the maximum depth of litter, which included leaves, twigs and bark from shrubs and trees, and detached groundstorey plant material, and the maximum height of herbaceous and woody vegetation, both with a ruler. For each of the 216 arena locations, we measured distance to the nearest shrub with a 30-m tape.

#### *Morphometric measurements*

Ants were identified using appropriate keys (Shattuck, 1999; Heterick, 2001, 2009; McArthur, 2007; Heterick & Shattuck, 2011), compared with specimens at the Australian Museum, and assigned to functional groups (Andersen's, 1995). Functional groups present in our study included cold climate specialists, dominant Dolichoderinae, generalised Myrmicinae, hot climate specialists, opportunist species and subordinate Camponotini. However, ant species from the genus *Monomorium* was not assigned to a functional group as this genera is difficult to identify to the level of species (Ayers *et al.*, 2001) and different species occur in multiple functional groups (Andersen, 1995). We used up to six individuals of each species to measure ant body size and to derive a body size index (BSI; Sarty *et al.*, 2006) calculated as head width  $\times$  hind femur length. This index was developed as a measurement of overall ant body size and relates to an ant's ability to penetrate gaps based on their length and width (Sarty *et al.*, 2006). Large indices therefore reflect larger-bodied ant species, whereas small indices reflect small-bodied species. Head width was measured as the maximum width of the head in full face view. We made linear measurements on dry pinned species using the Leica M125 dissecting microscope (Leica Microsystems, Wetzlar, Germany). For dimorphic species, only minor workers were used for measurements as major workers were rare (Gibb & Parr, 2010; Ossola *et al.*, 2015). We averaged BSI over each species.

#### *Resource monopolisation*

We used the number of individuals per species visiting the arena to assess whether vegetation complexity affected bait monopolisation, using the monopolisation index of Gibb and

Parr (2010). We considered a bait to be successfully monopolised when there were five or more individuals of the same species at a bait with no other species present. The monopolisation index was calculated as:

$$\text{Monopolisation index (MI)} = \text{abundance}_{\text{Sp.1}} \times \sqrt{\text{BSI}_{\text{Sp.1}}} - \sum \text{abundance}_{\text{Sp.i}} \times \sqrt{\text{BSI}_{\text{Sp.i}}}$$

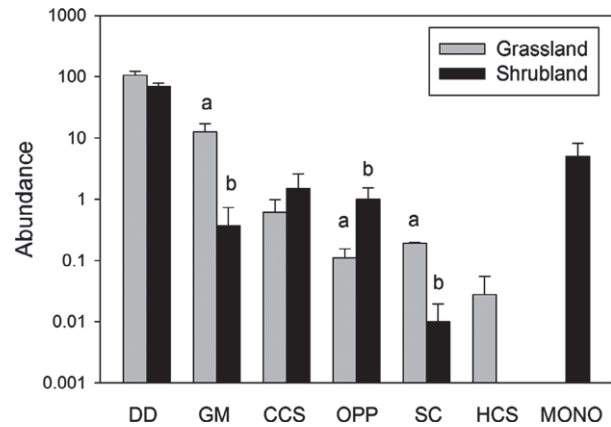
This formula incorporates the BSI to include the assumption that larger ant species need fewer workers to monopolise a resource than smaller ant species (Gibb & Parr, 2010). In the calculation of MI, sp.1 represents the dominant species, i.e. the one with the greatest abundance at the bait whereas sp. *i* represents other ants species present at the bait with fewer individuals.

### Statistical analysis

To test variation in ant species richness and functional group composition within the complexity arenas in relation to community (grassland versus shrubland), soil surface complexity, bait type and their two- and three-way interactions were explored using permutational multivariate analysis of variance with the Bray–Curtis similarity matrix in the PERMANOVA statistical package (Anderson *et al.*, 2008). The analysis examined multiple strata. The first stratum examined community effects, and the second stratum complexity effects, bait effects and their two- and three-way interactions with community and complexity. However, in this analysis, we were only interested in the community effect, i.e. whether there were ant compositional differences between grassland and shrubland complexity arenas. We used the same ANOVA structure with the MINITAB statistical software (Minitab, 2007) to test for differences in (i) abundance of the seven main functional groups within the complexity arenas, (ii) cover of bare soil, litter, biocrust and plants, (iii) litter depth, (iv) maximum vegetation height, and (v) distance to the nearest shrub, between grasslands and shrublands with site and block as random factors. Finally, we used the same ANOVA structure as described earlier to test whether complexity within the arenas influenced: (i) bait discovery time; (ii) body size index; and (iii) monopolisation of food resources (monopolisation index). For bait discovery time, time was converted from minutes to hours to meet normality assumptions. For the body size index model, differences in species composition or variability in foraging ant body sizes within species were not separated. Finally, for the monopolisation of food bait model, abundance of ants (by species) was capped at 100 individuals per arena to improve the normality of the data.

## Results

We recorded a total of 19 ant species from eight genera within our complexity experiment, with 17 species in the grassland arenas and 12 in the shrubland arenas. Mean species richness per arena was significantly higher in the grasslands (mean  $\pm$  SE;  $1.61 \pm 0.008$ ) than in shrubland ( $1.31 \pm 0.005$ ;  $F_{1,17} = 5.52$ ,



**Fig. 2.** Average functional group abundance ( $\pm$ SE) within the complexity arenas in grassland and shrubland. Functional groups are as follows: DD, dominant Dolichoderinae; GM, generalised Myrmicinae; CCS, cold climate specialists; OPP, opportunists; SC, subordinate Camponotini; HCS, hot climate specialists. MONO, ant genus *Monomorium*. Different letters indicate significant differences in functional group abundance between the two vegetation communities. No HCS were found in the shrubland, nor MONO in the grassland, arenas.

$P = 0.031$ ). However, there were no significant differences in overall species composition between the two communities (pseudo- $F_{1,10}$  (perm) = 0.68,  $P$ (perm) = 0.58), but generalised Myrmicinae ( $F_{1,10} = 9.85$ ,  $P = 0.006$ ) and subordinate Camponotini ( $F_{1,10} = 3.91$ ,  $P = 0.056$ ) were more abundant in grassland arenas, and opportunists ( $F_{1,10} = 5.13$ ,  $P = 0.038$ ) were more abundant in shrubland arenas (Fig. 2). Ant richness also differed in relation to complexity ( $F_{2,170} = 3.50$ ,  $P = 0.032$ ), with significantly greater richness in the control arenas ( $1.58 \pm 0.10$ ) than in high-complexity arenas ( $1.32 \pm 0.071$ ), and intermediate values in low-complexity arenas ( $1.49 \pm 0.084$ ). Ants from the genus *Iridomyrmex* occurred in all complexity treatment arenas and accounted for 90% of total abundance overall.

### Vegetation community complexity

Grasslands had more than twice the foliage cover of herbaceous plants as shrublands ( $F_{1,197} = 28.41$ ,  $P < 0.001$ ) and less bare soil ( $F_{1,197} = 15.01$ ,  $P < 0.001$ ), but there were no significant differences in biocrust cover, litter cover, or litter depth between communities ( $P > 0.05$ ; Table 1). Mean distance from an arena to the nearest shrub was 3.5 times greater in grasslands than in shrublands ( $F_{1,197} = 59.93$ ,  $P < 0.001$ ). Vegetation was significantly taller in shrublands (Table 1;  $F_{1,17} = 6.15$ ,  $P = 0.014$ ).

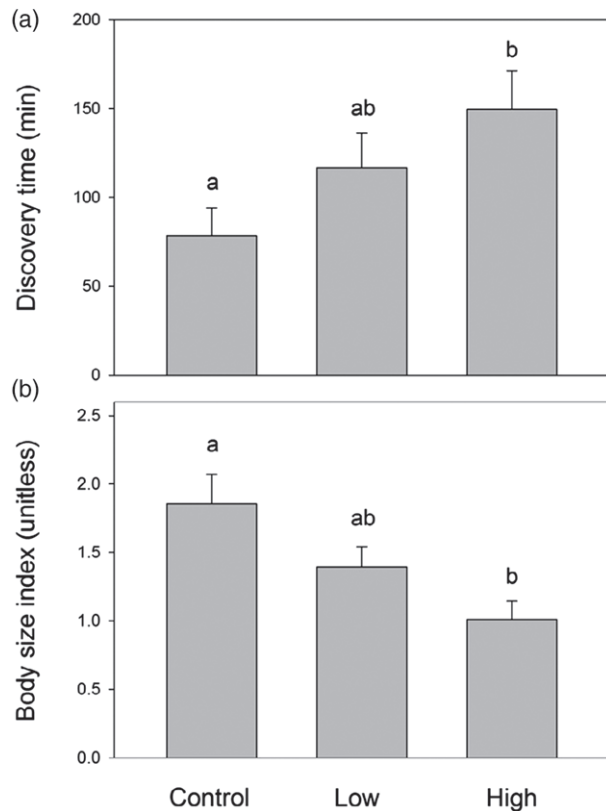
### Effect of complexity on foraging efficiency and ant body size

Ants took twice as long to find baits in high-complexity treatments (149.5 min) than in the control (71.7 min;  $F_{2,170} = 7.35$ ,  $P = 0.009$ ), with intermediate values for the low-complexity treatment (116.8 min; Fig. 3a). Bait discovery time did not differ

**Table 1.** Mean ( $\pm$ SE) values of the foliage cover of plants, cover of bare soil and biocrusts, litter cover and depth, maximum plant height, and distance of arenas to the nearest shrub in grasslands and shrublands.

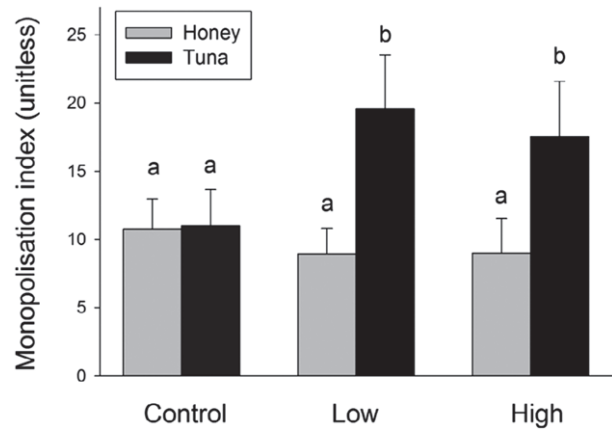
Attribute	Grassland		Shrubland	
	Mean	SE	Mean	SE
Foliage cover (%)	20.3 <sup>a</sup>	2.08	8.6 <sup>b</sup>	1.12
Bare soil cover (%)	18.4 <sup>a</sup>	2.07	28.7 <sup>b</sup>	2.32
Biocrust cover (%)	23.8 <sup>a</sup>	2.55	29.9 <sup>a</sup>	2.70
Litter cover (%)	37.9 <sup>a</sup>	2.95	32.4 <sup>a</sup>	2.83
Litter depth (mm)	9.5 <sup>a</sup>	1.50	7.4 <sup>a</sup>	2.25
Maximum vegetation height (m)	0.5 <sup>a</sup>	0.03	1.7 <sup>b</sup>	0.55
Distance to nearest shrub (m)	3.5 <sup>a</sup>	0.37	1.0 <sup>b</sup>	0.08

For a given attribute, different superscripts indicate a significant difference between grassland and shrubland.

**Fig. 3.** Mean ( $\pm$ SEM) discovery time (min) (a) and ant body size index (b) in relation to three levels of complexity. Different letters indicate significant differences among the three complexity levels at  $P < 0.05$ .

between vegetation communities or bait types, and there were no significant two- or three-way interactions between vegetation community, bait type, and complexity treatment.

Ant body size index declined with increasing habitat complexity ( $F_{2,170} = 7.88$ ,  $P = 0.005$ ). Ants that discovered baits in the high-complexity treatments were almost half the size (BSI =  $1.01 \pm 0.13$  mm<sup>2</sup>; mean  $\pm$  SD) of those that discovered baits in the control treatment (BSI =  $1.86 \pm 0.21$  mm<sup>2</sup>; Fig. 3b).

**Fig. 4.** Mean ( $\pm$ SEM) monopolisation index for two bait types in relation to three levels of complexity. Different letters indicate significant differences among the three complexity levels at  $P < 0.05$ .

Similar to discovery time, ant body size was unrelated to community or bait type or their two- and three-way interactions with complexity.

#### Effect of complexity on resource monopolisation

During the study, only four ant genera (*Iridomyrmex*, *Pheidole*, *Monomorium*, and *Camponotus*) successfully monopolised food resources. Over the 10-h period, 56% of baits ( $n = 122$ ) had been monopolised by a single ant species, and 27% ( $n = 58$ ) had not been visited by any ants. The remaining 17% of baits either had fewer than five individuals from the one species or two or more different species of ants were present at the bait with a similar number of individuals. Of the 122 monopolised baits, *Iridomyrmex* species successfully dominated 87.7% of food resources, followed by *Pheidole* (6.6%), *Monomorium* (4.1%), and *Camponotus* (1.6%). The high monopolisation rate in the genus *Iridomyrmex* was driven by one species, *Iridomyrmex calvus*, which successfully monopolized 71 resource baits.

We found a significant bait effect ( $F_{1,199} = 12.03$ ,  $P < 0.001$ ) and a borderline bait  $\times$  treatment interaction ( $P = 0.059$ ), with no difference in the monopolisation index of baits in the controls, but significantly greater monopolisation of the tuna in low- and high-complexity arenas (Fig. 4). Monopolisation of food resources did not differ between grassland and shrubland.

## Discussion

Habitat complexity shapes ant communities by influencing mobility and thus foraging efficiency, interspecific competition for communal food resources, and the likelihood of encountering predators (Gibb & Parr, 2010; Wilkinson & Feener, 2012). We examined whether changes in soil surface complexity affected ant foraging efficiency, body size, and monopolisation index within two vegetation communities of markedly different structure. We found that ant richness was significantly

greater in grassland arenas, and there were some differences in functional group composition between the shrubland and grassland arenas. Ground surface complexity significantly affected bait discovery time and body size. Ants took longer to discover baits in more complex environments, and ant body size declined with increasing complexity, consistent with the size-grain theory (Kaspari & Weiser, 1999). Monopolisation was greater on tuna than on honey, but only under low and high complexity. However, vegetation community did not influence foraging efficiency, body size index, or monopolisation despite some differences in vegetation cover. Our study illustrates that ant foraging abilities are more responsive to changes in complexity at smaller spatial scales than changes over larger scales associated with a conversion of grassland to shrubland.

#### *Ant richness and functional group composition*

We found that ant richness was significantly greater in the grassland than in shrubland arenas. These results differ from previous studies showing that ants richness was either unaffected or greater under low levels of shrub encroachment characterised by grassland with a few scattered shrubs (e.g. Bestelmeyer, 2005; Blaum *et al.*, 2009; Dahms *et al.*, 2010). Higher ant richness in our grassland arenas coincided with greater plant cover, potentially allowing submissive species to co-occur with dominant species. Greater plant cover would make it more difficult for dominant species to defend scarce resources in more complex habitats and would result in fewer interactions among submissive and dominant species (Sarty *et al.*, 2006).

Although we detected no significant differences in overall species composition between grassland and shrubland arenas, the functional groups generalised Myrmicinae and subordinate Camponotini were more abundant in grasslands, and the opportunists more abundant in our shrublands. Subordinate Camponotini have been shown to be more abundant in woodlands than in grasslands (Gómez *et al.*, 2003), potentially because they support a greater number of extrafloral nectaries and nesting sites for these ants. Greater abundance of subordinate Camponotini in grassland arenas suggests a preference for habitats with greater vegetation cover, as these ants are behaviourally submissive in the presence of the dominant *Iridomyrmex* species (Andersen, 1995). The greater abundance of opportunists in shrubland arenas is consistent with the notion that this functional group prefers disturbed habitats such as shrublands with less plant cover and more bare soil supporting a less diverse ant community (Hoffmann & Andersen, 2003). Overall, however, despite the large coverage of bare soil in shrublands (28% of the community), ants may not perceive shrublands as less complex than grasslands due to patches of litter, logs, and biocrust that characterise some of these shrublands (Eldridge *et al.*, 2013).

#### *Habitat complexity influences foraging efficiency*

Ants took twice as long to find baits in the high-complexity treatments than in either the control or low-complexity treatments, consistent with our first hypothesis. The design of our experimental arenas meant that ants could not walk across

the surface, but were forced to move through the substrates. Although our method may underestimate what happens under natural conditions, its advantage was that it allowed us to test the effects of different levels of substrate naturally occurring in grassland and shrublands on ant foraging behaviour, and test potential interspecific interaction and competition for shared resources. Longer foraging times under high complexity probably reflect hindered movement, as vegetation structure is known to affect ant movement and foraging distance (Crist & Wiens, 1994). For example, the harvester ant, *Pogonomyrmex occidentalis* is known to prefer cleared paths over vegetated paths (Fewell, 1988a). This increases the speed at which they can forage, allowing them to forage further and for longer (Fewell, 1988b). Similarly, larger patches of bare soil at grazed sites allow *P. occidentalis* to forage further than they could at ungrazed sites (Usnick, 2000).

For ants, the energetic cost of foraging is considered minimal compared with the energetic gains from the food resources (Fewell, 1988b; Baroni-Urbani & Nielsen, 1990; Weier & Feener, 1995). Time costs of foraging, however, are considered much more important when maximising net resource intake over time, and are more influential in determining foraging behaviour (Weier & Feener, 1995; Morehead & Feener, 2009). Thus, ants may prefer to forage in simple habitats as it is more time-efficient and allows them to make multiple trips with food resources back to the nest, thus increasing the net gain per trip. For example, the harvester ant *P. occidentalis* collects significantly more food resources along a cleared path than a vegetated path (Fewell, 1988b), thereby increasing the net gain of the foraging trip. Shorter discovery times in the control treatment could also reflect differences in the body size of ants. The running speed of ants is a function of hind leg length and body mass (Hurlbert *et al.*, 2008). Larger ant species tend to have longer legs (Pearce-Duvel *et al.*, 2011), which are ideal for locomotion in planar environments, as stride length is proportional to leg dimensions (Zollikofer, 1994), and larger-bodied species require fewer steps to cover the same distance than small-bodied species (Lipp *et al.*, 2005). This can result in shorter bait discovery times for large ant species within planar environments such as the soil surface. Our study shows that ants are more efficient at locating resources in simple environments than in high-complexity environments, which hinder their movement regardless of ant body size.

#### *Habitat complexity affects ant body size*

Size-grain theory suggests that, as the body size of terrestrial organisms declines, their environment becomes less planar and more rugose (Kaspari & Weiser, 1999). Large ant species with long legs perceive their environment as more planar and can travel over complex landscapes, reducing the cost of locomotion (Sarty *et al.*, 2006). Small-bodied ants with short legs, however, are able to navigate through more complex environments such as leaf litter (Wiescher *et al.*, 2012), in which their large-bodied counterparts have impeded movement. We found that ant body size index declined with increasing habitat complexity, supporting our second hypothesis and consistent with size-grain theory.

Ants that discovered baits in the high-complexity treatment were approximately 44% smaller than ants that discovered baits in the control treatment. Previous studies have shown mixed effects of complexity on body size. For example, tropical leaf litter ants that first detected and accessed baits in the most rugose landscape were 42% smaller than those that detected baits in planar environments (Farji-Brener *et al.*, 2004), supporting our findings. Studies by Gibb and Parr (2010) showed that ant body size was larger in simple, rather than complex, environments and microhabitats. However, within urban environments, body size and morphological traits were unrelated to differences in habitat complexity within low-complexity and high-complexity parks, and high-complexity woodland remnants (Ossola *et al.*, 2015). Our results support the notion that smaller ants are more efficient at foraging between leaf litter, whereas larger ants are more successful at foraging in more planar environments.

#### *Habitat complexity alters resource monopolisation*

Contrary to the third hypothesis, habitat complexity had no effect on resource monopolisation within grassland and shrubland communities. We predicted that the monopolisation index would be higher in the simpler shrubland environments that are typified by large patches of bare soil (Eldridge *et al.* 2014, 2015). Monopolisation of food resources declines with increasing complexity as food resources are easier to find and dominate in simple environments, particularly for dominant ant species (Parr & Gibb, 2012). Complex environments, however, minimise the opportunity for dominant and subordinate species to interact, allowing them to coexist through different resource availability based on their body size (Sarty *et al.*, 2006). The lack of a difference between shrubland and grassland could have resulted from the fact that the dominant Dolichoderinae genus *Iridomyrmex* monopolised 89% of the discovered food baits and had similar abundance in grassland and shrubland complexity arenas. This *Iridomyrmex* effect was driven by *I. calvus*, which successfully monopolised 72 resource baits and was present in all complexity treatments. *Iridomyrmex calvus* prefer cool and moist conditions that typify well-shaded forests (Majer *et al.*, 2013). Similar abundance of *I. calvus* between grassland and shrubland arenas may have occurred because the grasslands in our study had a continuous herbaceous understorey layer that provided adequate shade and therefore cooler conditions for this species. *Iridomyrmex* species are known to be highly active and aggressive towards other ant species, thereby suppressing the abundance and diversity of other ant species (Andersen & Patel, 1994). Additionally, *Iridomyrmex purpureus* is highly efficient at locating and protecting food resources compared with other ant species, and can successfully displace other ant species (including other *Iridomyrmex* species) at food baits without being displaced itself (Gibb & Hochuli, 2004).

Monopolisation of tuna by ants was greater under both low and high complexity, but not significantly different to honey baits in the control arenas (Fig. 4). Higher monopolisation of tuna baits was expected as ants show a preference for protein resources when carbohydrate-rich resources are easily accessible (Kay,

2004). Furthermore, the tuna bait contains protein, salts, water and fats, which attract both solid and liquid feeders (Delsinne *et al.*, 2007). However, tuna has been found to attract dominant species such as *I. purpureus* from greater distances than naturally occurring baits such as mealworms (Gibb, 2005), thereby influencing observed interspecific interactions. This may occur as tuna has a greater olfactory intensity than honey, thus attracting more ants from further away. Thus, some of the interactions observed in this study may not represent those that occur naturally, as many ant species that would not normally compete for shared resources would have had to interact with aggressive *Iridomyrmex* species.

#### Conclusions

Overall our study shows that ants are responsive to changes in habitat complexity, operating at small spatial scales. Thus naturally occurring soil surface features such as leaves and twigs act as an environmental filter by altering foraging success of ants of a particular body size (Donoso, 2014). Our results indicate that resources are easier to find in simple than in complex environments, especially for large ant species. Large-bodied and long-legged species are more efficient at foraging in planar environments, whereas their small-bodied conspecifics are efficient at foraging in more complex habitats, consistent with size-grain theory. While we found no evidence that habitat complexity affected monopolisation of resources within grassland and shrubland communities, resource type and availability may be more influential in both vegetation communities.

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