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Original Article

Habitat complexity affects functional traits and diversity of ant assemblages in urban green spaces (Hymenoptera: Formicidae)

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Abstract

Habitat complexity conferred by vegetation characteristics mediates key processes that govern the assemblage of insect communities. Thus, species within the community should only persist if their functional traits are well-matched to the conditions of their environment. Here, we compared ant assemblages between habitats in terms of species richness and functional-trait distribution at the species and the assemblage level. Ants were collected from 36 sites representing different degrees of habitat complexity mediated by standing vegetation. We found fewer ant species in simpler habitats, supporting the "habitat-heterogeneity" hypothesis. We measured key functional traits of ants that reflect their foraging and dispersal strategies, such as body size, femur length, antenna scape length, and head length / width. Interactions of species traits with measured habitat complexity variables were assessed at the species and the assemblage level using a fourth-corner approach. Ant traits were closely related to environmental complexity. In wooded habitats, ants were larger and had broader heads, while ants with longer antenna scapes prevailed in habitats with a dense herb / grass layer. Our study suggests that vegetation structural complexity can act as an environmental filter, driving ant assemblages in terms of both species numbers and functional traits. Our results can be used to predict turnover patterns in ant assemblages due to changes in management practices.

Key words: Ant assemblages, functional traits, fourth corner, habitat complexity.

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Introduction

Species assemblages vary greatly across different biomes, regions and habitat types. One of the main challenges in modern community ecology is identifying the factors and mechanisms that shape biotic assemblages, in terms of both composition and functional structure (McGill & al. 2006, Agrawal & al. 2007). As species-diversity descriptions of community composition neglect functional aspects, they are increasingly complemented by trait-based approaches to gain a better understanding of functional community structure and responses to environmental change (McGill & al. 2006, Agrawal & al. 2007, Shipley 2010, Segar & al. 2013). Using such species trait-environment relationships, a multitude of studies have reported that communities respond to environmental change (and often which species respond) (Ribera & al. 2001, Birkhofer & al. 2017). However, few studies of insect communities have investigated *how* they change (but see Gibb & al. 2015). This is a longstanding issue in ecology as species traits and environmental variables are hard to associate with species abundance (or occurrence) data (Legendre & al. 1997). Recently, Brown & al. (2014) developed a statistical approach to find a model-based solution to this so-called fourth-corner problem; abundance (L), trait (Q) and environment (R) data are combined to determine a matrix describing the trait-environment relationship (D), aimed at understanding how species traits are associated with the environment.

Habitats usually vary in their amounts of standing vegetation, rock formation, soil and litter on the ground, leading to variations in complexity or heterogeneity. The "habitat heterogeneity hypothesis" (MacArthur & MacArthur 1961, MacArthur & Wilson 1967) proposes that more structurally complex habitats can provide a greater variety of niches and resources, thus supporting more species. Habitat complexity conferred by the physical structure of standing vegetation is positively related to the diversity of many taxa, including birds, reptiles, amphibians and insects, but has also shown negative relationships with small mammals and butterflies (Tews & al. 2004). These idiosyncratic species responses elevate the need to investigate the effects on a highly responsive and cosmopolitan bio-indicator taxon – the ants.

Ants are ideal organisms for assessing relationships between habitat, species diversity and functional traits, as they are found in virtually every terrestrial ecosystem and play a crucial role by performing multiple ecosystem services, thereby regulating fundamental ecological processes (Hölldobler & Wilson 1990, Folgarait 1998, Peters & al. 2016). As valuable ecosystem engineers, ants scavenge for dead insects, prey on potential insect pests, pollinate plants, aerate the soil and foster nutrient cycling (Folgarait 1998, Philpott & Armbrecht 2006). Ant assemblages are shaped by environmental factors at multiple scales, ranging from larger global / landscape-scale factors such as climate (Dunn & al. 2009, Gibb & al. 2015), elevation (Sanders & al. 2007, Bernadou & al. 2014) and habitat type (Bihn & al. 2010, Calcaterra & al. 2010) to smaller, local-scale factors like patch size (Gibb & Hochuli 2002) and habitat complexity (Andersen 1986, Lassau & Hochuli 2004, Gibb & Parr 2010, 2013). Species richness and diversity of ant communities have been found to increase with temperature and decrease with precipitation (Dunn & al. 2009) and elevation (Bernadou & al. 2014), but ants are also prone to environmental disturbances and are thus widely used as bioindicators for ecosystem health and functioning (Andersen & al. 2002, Andersen & Majer 2004, Underwood & Fisher 2006).

The ant fauna responds to habitat heterogeneity at two spatial scales. On the landscape scale, ant diversity is positively associated with forest area (Spiesman & Cumming 2008, Dauber & al. 2011, Ahuatzin & al. 2019) and shrubby landscapes (Bestelmeyer & Wiens 2001). On the local scale, ant species richness is higher at high complexity forest sites as compared to heath (Andersen 1986), prairie or pasture sites (Hill & al. 2008). However, negative associations between ant species richness and diversity with habitat complexity in terms of tree cover, shrub and herb understorey have also been found in forests (Ahuatzin & al. 2019), open woodlands (Lassau & Hochuli 2004) and urban green spaces (Ossola & al. 2015). As the effects of habitat complexity on the ant fauna thus appear to be inconsistent, we therefore examine whether more complex habitats in urban green spaces support more diverse and species-rich ant assemblages.

For small, walking animals like ants, the structural complexity of the substrate may also be important for anatomical traits. Ants walk differently on open, planar surfaces like desert ground or through grasslands or woodlands with many grass stems or woody twigs, where their movements are impeded. Thus, Kaspari & Weiser (1999) devised the "size-grain hypothesis", predicting that ants in planar environments should have relatively longer legs and be larger than ants in more complex environments. Several studies have tested this hypothesis by looking at ant traits – different measures of body size and femur length – in relation to habitats with different degrees of structural complexity. Larger ants prevailed in more open habitat types with less shrub cover in Australia (Gibb & al. 2015), South Africa (Gibb & Parr 2010), and Spain (Arnan & al. 2013). Similarly, successful foragers were smaller in highly complex baited arenas filled with fine materials (Sarty & al. 2006, Gibb & Parr 2013). Other studies did not identify any relationship between body size and ground cover complexity in native Flatwoods in Florida (Wiescher & al. 2012) or in urban green spaces in Australia (Ossola & al. 2015). Based on these inconsistent results between studies, the overall picture is far from clear.

Urban habitats, large green spaces such as public parks and golf courses are increasingly used as study systems to assess species diversity and drivers of biotic communities for a variety of taxa. Studies have targeted single groups, such as plants (Threlfall & al. 2016a), insects (Christie & Hochuli 2008), mammals (Gallo & al. 2017), birds and bats (Threlfall & al. 2016b) as well as groups of taxa, for example, plants, birds and ants (Nooten & al. 2018). Common management practices in these green spaces – for example, vegetation clearing, litter removal, planting and mowing – shape the structural complexity and also act as disturbance factors (Byrne 2007). This makes urban green spaces an ideal study system for testing long-standing ecological hypotheses in the field. Moreover, with ever increasing urbanisation, these are key habitats for biodiversity in many parts of the world.

This study aims to investigate the relationships between structural vegetation complexity and ant traits on the species and the assemblage level. Though many traits can be considered for such assessments, most studies consider "whole-body" traits, as they are thought to be important for survival, foraging and reproduction (Jensen & Holm-Jensen 1980, Farji-Brener & al. 2004, Gibb & Parr 2013). In ants, these generally include body size, length of dispersion-related appendages (e.g., legs or wings) and the size, shape or position of sensory appendages (e.g., eyes, antennae), which are important for perceiving the environment and locating resources or prey items (Weiser & Kaspari 2006, Silva & Brandão 2010). We use a particularly informative method, the fourth-corner approach (Brown & al. 2014), to assess whole-body trait variation in ant assemblages.

The following questions were addressed:

1) Do complex urban habitats harbour more ant species? This tests the "habitat heterogeneity hypothesis"

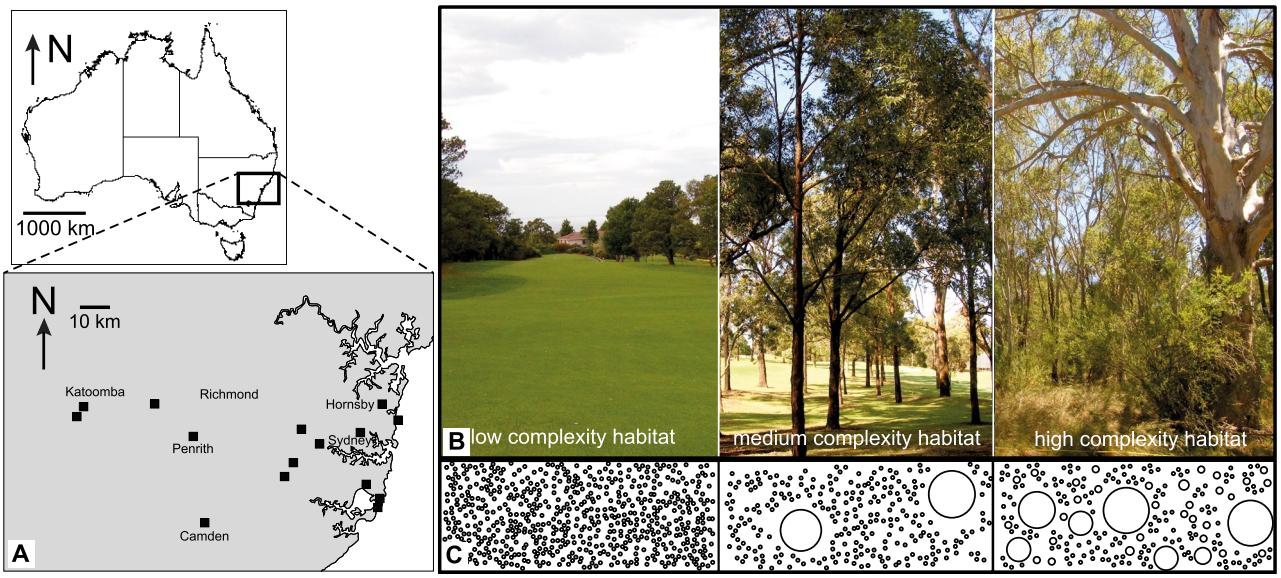

Fig. 1: (A) Locations of golf courses (filled squares) within the Greater Sydney area in southeast Australia; (B) three habitat types representing low, medium and high habitat complexity; (C) Graphical representation of the surface covered by standing vegetation: grass (small circles) shrubs (medium circles) and trees (large circles) in each habitat.

put forward by MacArthur & MacArthur (1961) and MacArthur & Wilson (1967).

2) Is there a general relationship between ant functional traits and vegetation structure in habitats?

3) Do complex habitats harbour smaller ant species with shorter legs? This tests the "size-grain hypothesis" put forward by Kaspari & Weiser (1999).

Based on current knowledge, we hypothesise that more ant species will be found in more complex habitats, supporting the "habitat heterogeneity hypothesis". We further predict that the distribution of ant traits will (i) change with habitat complexity for single species traits and the ant assemblage as a whole, and (ii) support the "size-grain hypothesis".

Methods

The data presented here were collected as part of a larger study assessing drivers of biodiversity on urban golf courses in the Greater Sydney Region (Nooten & al. 2018).

Study area: We selected 15 golf courses in the Greater Sydney Region in south-east Australia covering a range of course characteristics including age, size, vegetation types and degree of connectivity to adjacent native habitat (Fig. 1A). Selected courses spanned an area of ~ 88 km east-west and ~ 50 km north-south. Sites ranged longitudinally from coastal Dee Why (33° 44' 20.75" S, 151° 18' 22.06" E) to Wentworth Falls (33° 41' 48.18" S, 150° 21' 45.98" E) in the Blue Mountains, and latitudinally from Terrey Hills (33° 41' 19.56" S, 151° 15' 38.52" E) in the north, to Camden (34° 3' 1.19" S, 150° 43' 51.29" E) in the south.

Study design: To assess the relationship between the ant fauna and habitat complexity we sampled from three different habitat types within each golf course: fairways, between-fairway and remnant vegetation. These habitats differ in the presence / absence and abundance of three vegetation layers: trees, shrubs and herbs, resulting from golf course landscaping, planting and maintenance (see Fig. 1B, C). Habitat types can be considered as coarse categories of habitat complexity conferred by different numbers of vegetation layers. This somewhat subjective classification of complexity was used only for our species richness and diversity analyses, as these require categories for comparison. For assemblage composition, species trait and assemblage trait analyses, we measured continuous quantitative habitat complexity variables (see below).

For each habitat type, four replicates per golf course were selected using a stratified randomised approach: a grid of 50 x 50 m cells was superimposed on maps of the golf courses and four sites per habitat type were randomly drawn from available grid cells. A total of n = 168 collection sites in habitats with similar size and shape were selected: 12 golf courses contained all three habitat types, resulting in 12 courses × 3 habitats × 4 replicates (n = 144 sites); at three golf courses remnant habitats were absent, resulting in an additional 3 courses × 2 habitats × 4 replicates (n = 24 sites).

Habitat complexity variables: We selected seven habitat variables to be measured at each site adjacent to the ant collection transect. Variables were selected to capture the habitat complexity: (1) tree biomass (t ha^{-1}), (2) tree density (number of trees ha^{-1}), (3) shrub biomass (t ha^{-1}), (4) shrub density (number of shrubs ha^{-1}), (5) Herb biomass (t ha^{-1}), (6) herb height (cm) and (7) herb cover (%). Tree parameters were measured within a 10 × 40 m rectangular survey plot, while shrub and herb parameters were assessed in smaller (2 × 2 m) subplots (two per survey plot). Tree diameter (diameter at breast height) was measured for

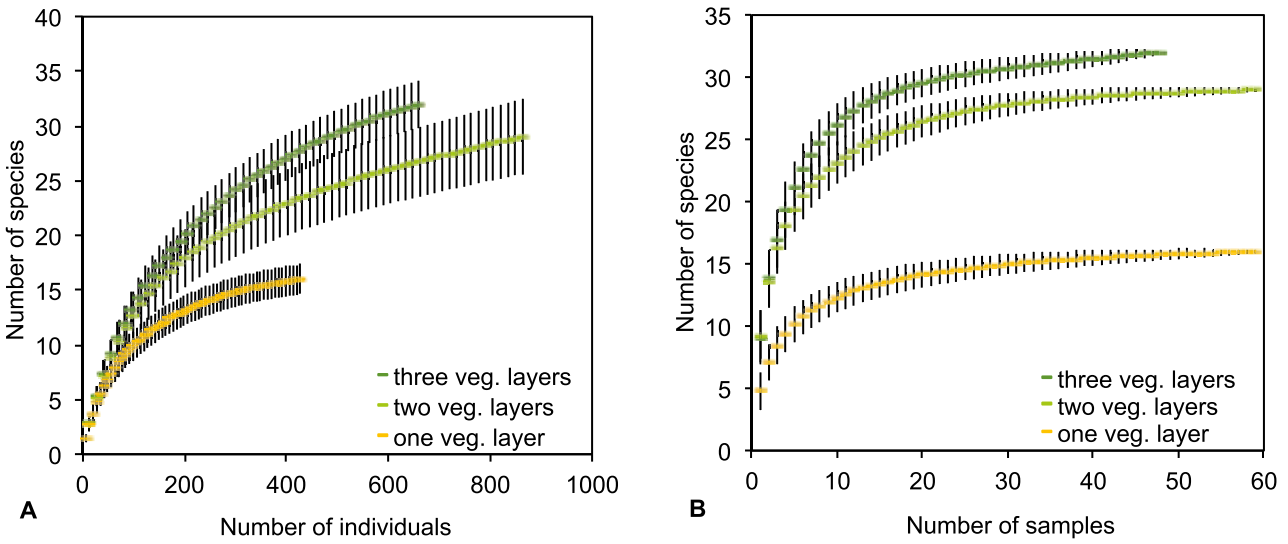

Fig. 2: (A) Coleman's rarefaction and (B) species accumulation curves. Ant species richness based on the number of (A) individuals ± SD, and (B) samples in three habitat types according to the number of vegetation layers (one, two, three veg. layers).

all trees present in the plot; those with diameter < 10 cm were regarded as shrubs. Shrub diameter was measured for all shrubs present in subplots (at 10 cm above ground). Field measurements of tree and shrub diameter were then used to calculate their respective biomasses, using published data on allometric relationships between biomass and diameter values (Paul & al. 2013). Herb height was measured at five points in each subplot, at each corner and in the centre; herb cover was estimated as % cover of herbs and grasses combined, the latter being dominant in golf course habitats. Herb biomass was calculated using a function, previously obtained by regressing biomass vs. herb height for a subset of samples, and then corrected by % cover.

Ant surveys: Ants were collected once between January and April 2014 using minced meat baits, following preliminary trials of different collection methods. Pitfall trapping, a more preferred method, could not be used, as digging holes was not feasible on the participating golf courses. At each site, five baits in 1.5 ml Eppendorf tubes were deployed at 20 m intervals on the ground along a 100 m transect per replicate and left out in the morning for three hours (09.00 - 12.00 h). Tubes were retrieved by quickly adding 70% ethanol before closing the lid. A total of 60 tubes per course (three habitats × four replicates × five tubes) were collected. Samples were stored in 70% ethanol in the freezer at -20 °C. Collecting ants in this fashion introduced certain caveats. This approach did not allow for sampling of the entire fauna, but rather focused on meat-attracted species belonging to predator and scavenger feeding guilds, and those active during the day. Individual tubes yielded from 1 to > 50 ants and from 1 - 3 species. Nevertheless, sampling ants using baits is suitable for comparing ant diversity and functional traits among distinct habitats or conditions (Lopes & Vasconcelos 2008, Bestelmeyer & Rio Casanova 2009, Campbell & al. 2015).

Ant processing and identification: Ants were separated from baits, washed and stored in 70% ethanol. Ants were first sorted to genus and then to species level. Identification to subfamily / genus level was carried out using taxonomic keys (Andersen 1991, Shattuck 1999) and online identification resources (http://www.antwiki.org/wiki/). Final species identification was carried out in Darwin, Australia, under expert guidance of Alan Andersen and the use of the CSIRO ant reference collection. Dried and mounted voucher specimens have been lodged there as a reference.

Morphometric ant measurements: Six workers per species (or fewer if only four or five were collected) were randomly selected to carry out a set of five morphometric trait measurements; the mean thereof was used as a value for each species. Only minor workers were selected in species with minor and major, that is, worker and soldier castes. Sample location was not considered in the selection of the individual workers. Also, no measurements were performed for species with fewer than four individuals, or which occurred in less than three sample vials, as these were considered as transients.

Traits were selected following previous studies, where they had shown ecological relevance (e.g., Weiser & Kaspari 2006, Schultheiss & al. 2012, Gibb & al. 2015, Ossola & al. 2015), and in coherence with our hypotheses. We measured head width (HW), head length (HL), femur length (FL), antenna scape length (SL) and Weber's length of the alitrunk (WL, Weber 1983). As the alitrunk is rigid, WL is a useful measure of relative body size and is measured from the anterior edge of the pronotum to the posterior corner of the metapleuron, as in previous allometric studies of *Cataglyphis*, *Ocymyrmex*, and *Melophorus* species (Schultheiss & al. 2012, Sommer & Wehner 2012, Gibb & al. 2015). Femur and antenna scape measurements were taken in planar view. Head measurements were taken

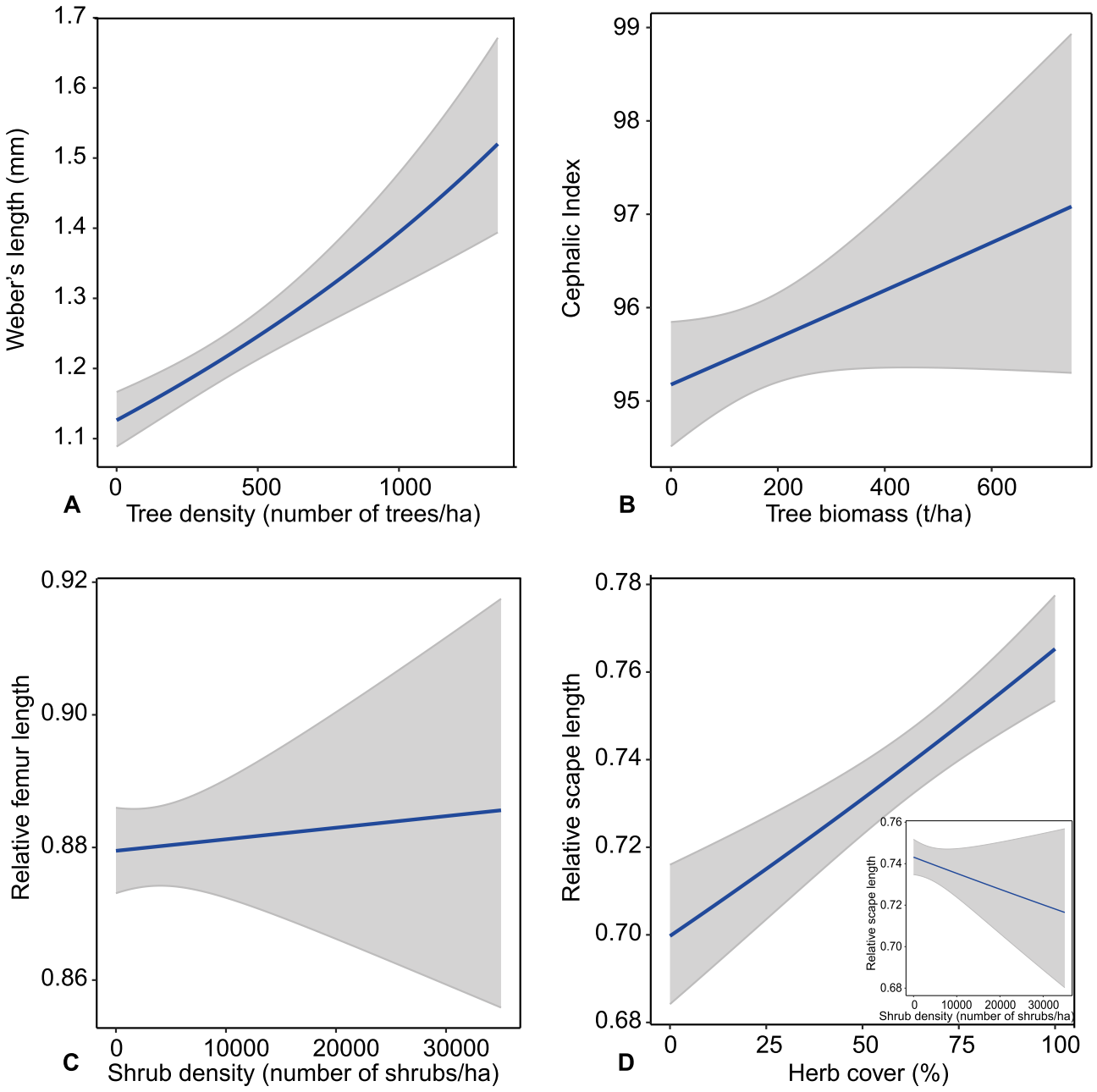

Fig. 3: Relationships between ant traits and environmental variables. (A) Weber's length, (B) cephalic index, (C) relative femur length, and (D) relative scape length; Solid blue lines show significant relationships between traits and variables (at $P < 0.05$), grey shaded area shows 95% confidence interval.

in full frontal view; HW was measured as the maximum width excluding the eyes, HL was measured from the most anterior point of the clypeus to a line perpendicular to the most posterior point of the head. A total of 1,170 measurements (39 species × 6 individuals × 5 traits) were taken, using a binocular microscope and software INFINITY ANALYZE (Lumenera corp., Ottawa, ON) to take photographs and measurements, with an accuracy of ~ 0.01 mm.

As our aim was to analyse these functional trait measures in relation to habitat type and environmental variables, we assessed co-linearity between morphological measures by calculating Pearson's *r*. Absolute measures of FL, SL, HW and HL were all strongly correlated with WL (r = 0.87 - 0.97). We therefore normalised measures of FL and SL to body size by dividing them by WL, thus obtaining relative femur length (RFL) and relative scape length (RSL) (Gibb & Parr 2013, Gibb & al. 2015). As HW and HL measures are less informative than overall head shape in regard to dietary adaptations (Kaspari 1993, Sarty & al. 2006, Holley & al. 2016), we analysed these measurements in the form of a cephalic index (CI), calculated as: CI = 100 HW / HL. The traits we used in all analyses are therefore WL, RFL, RSL, and CI.

Tab. 1: Summary of generalised linear mixed modelling (GLMM) for (A) Weber's length (WL), (B) cephalic index (CI), (C) relative femur length (RFL) and (D) relative scape length (RSL). Shown are the model coefficient (Estimate), standard error (*SE*), *t*-value, partial *P* (*p*-value) of the *F*-Statistic. Bold values indicate statistical significance. [a] Note: Number of observations (n = 485); number of groups (n = 15); degrees of freedom (n = 464).

Parameter	**Estimate** [a]	***SE***	***t*-value**	***p*-value**
(A) Weber's length				
Intercept	8.73^{E-04}	4.51^{E-05}	19.382	**<0.0001**
Tree biomass (t ha^{-1})	2.77^{E-08}	8.40^{E-08}	0.330	0.7413
Tree density (tree ha^{-1})	-1.78^{E-07}	4.84^{E-08}	-3.680	**0.0003**
Shrub biomass (t ha^{-1})	1.29^{E-06}	4.69^{E-06}	0.276	0.7827
Shrub density (shrub ha^{-1})	-2.10^{E-09}	3.15^{E-09}	-0.677	0.4989
Herb height (cm)	5.07^{E-07}	1.05^{E-06}	0.482	0.6302
Herb cover (%)	1.72^{E-07}	5.02^{E-07}	0.342	0.7326
(B) Cephalic index				
Intercept	1.05^{E-02}	1.25^{E-04}	84.238	**<0.0001**
Tree biomass (t ha^{-1})	-6.30^{E-07}	2.09^{E-07}	-3.017	**0.0027**
Tree density (tree ha^{-1})	2.39^{E-07}	1.24^{E-07}	1.934	0.0537
Shrub biomass (t ha^{-1})	-1.08^{E-06}	1.18^{E-05}	-0.092	0.9269
Shrub density (shrub ha^{-1})	-6.00^{E-09}	8.34^{E-09}	-0.732	0.4647
Herb height (cm)	3.47^{E-07}	2.73^{E-06}	0.127	0.8990
Herb cover (%)	1.77^{E-07}	1.29^{E-06}	0.137	0.8912
(C) Relative femur length				
Intercept	1.135	1.79^{E-02}	63.523	**<0.0001**
Tree biomass (t ha^{-1})	-1.17^{E-05}	3.16^{E-05}	-0.369	0.7122
Tree density (tree ha^{-1})	1.20^{E-05}	1.95^{E-05}	0.616	0.5381
Shrub biomass (t ha^{-1})	3.35^{E-03}	1.83^{E-03}	1.827	0.0684
Shrub density (shrub ha^{-1})	-3.30^{E-06}	1.26^{E-06}	-2.641	**0.0085**
Herb height (cm)	3.83^{E-04}	4.17^{E-04}	0.920	0.3579
Herb cover (%)	-6.50^{E-05}	1.96^{E-04}	-0.332	0.7401
(D) Relative scape length				
Intercept	1.386	3.26^{E-02}	42.524	**<0.0001**
Tree biomass (t ha^{-1})	-3.63^{E-05}	5.58^{E-05}	-0.651	0.5154
Tree density (tree ha^{-1})	6.94^{E-05}	3.57^{E-05}	1.947	0.0521
Shrub biomass (t ha^{-1})	6.50^{E-03}	3.38^{E-03}	1.921	0.0554
Shrub density (shrub ha^{-1})	-5.60^{E-06}	2.30^{E-06}	-2.422	**0.0158**
Herb height (cm)	8.48^{E-04}	7.64^{E-04}	1.110	0.2677
Herb cover (%)	-9.14^{E-04}	3.56^{E-04}	-2.564	**0.0107**

Data analyses: Species richness and diversity. To assess whether more complex habitat types harboured a more diverse and species-rich ant fauna, we compared species richness and diversity among the three habitat types. The Chao-1 index (Chao 1984) was calculated as an estimator for species richness and adequacy of sampling, and the inverse Simpson's index (1 / D) as diversity index (Magurran 2004, Simpson 1949). Species rarefaction and accumulation curves (Gotelli & Colwell 2001) were generated in the program EstimateS 8.2 (Colwell 2013).

Species traits and habitat complexity. Statistical analyses were conducted in *R* v3.2.4 (R Development Core Team 2017). To assess whether there was an association between species traits and any of the seven habitat variables, we firstly assessed co-linearity of the latter by calculating Pearson's *r*. Herb biomass and height were highly correlated (r = 0.90); herb biomass was therefore eliminated from the list of considered variables. We performed generalised linear mixed modelling (GLMM) in the package *MASS* (Venables & Ripley 2002). The function "*glmmPQL*" with a "Gamma" distribution was

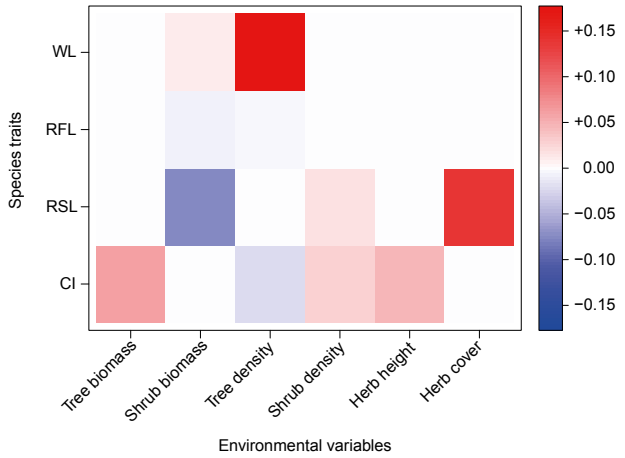

Fig. 4: Fourth-corner plot: Interaction coefficients between species traits (y-axis) and environmental variables (x-axis) among ant assemblages based on abundance are shown. Significant associations are shown in red (positive) and blue (negative). Colour intensity represents interaction strength (coefficient values on log scale). Environmental variables are: tree biomass (t ha^{-1}), shrub biomass (t ha^{-1}), tree density (number of trees ha^{-1}), shrub density (number of shrubs ha^{-1}), herb height (cm) and herb cover (%). Ant traits are Weber's length (WL), relative femur length (RFL), relative scape length (RSL) and cephalic index (CI).

used, which allows the fitting of mixed-effects models for random (nested = golf course) and fixed effects (= habitat variables) (Zuur & al. 2009). Alpha was set at 0.05 for all statistical tests.

Assemblage composition. Differences in species composition in relation to the six habitat variables were analysed using the multivariate extension of generalised linear models "*manyglm*" (Warton & al. 2012) in the package *mvabund* (Wang & al. 2017). Frequency of occurrence data were analysed using a negative binomial distribution and the "block" function to account for the nesting of sites within golf courses. The "drop1" function was used to find the most parsimonious model. The multivariate *Wald* χ^2 test statistic was used to evaluate differences between sites.

Assemblage trait structure – fourth corner. To assess relationships between species traits and the environment at the assemblage level, a fourth-corner model approach was used (Brown & al. 2014). This approach extends the previous analyses, which estimate relationships between species traits and habitat variables at a species level, by relating single traits to individual species (see above). Here, the fourth-corner analysis considers interactive effects by accounting for all species together, rather than examining one species at a time (Brown & al. 2014, Gibb & al. 2015). We used three tables: species frequency data (*L*), environmental habitat variables (*R*) and species traits (*Q*) in a fourth-corner analysis (Brown & al. 2014) using "*traitglm*" with a negative binomial distribution in the package *mvabund* (Wang & al. 2017). Environmental and trait variables were standardised by subtracting the mean and diving by standard deviation, to allow interpretation of coefficient sizes directly in terms of interaction strength and importance. This fourth-corner model provides information on *how* species traits and environmental variables are associated, by providing coefficient values that quantify strength and direction of associations, which are either negative (blue in Fig. 4) or positive (red). For example, a positive association of WL and tree density shows that there are more large ants at sites with high tree density. The function "*glm1path*" and the least absolute shrinkage and selection operator (LASSO) was used to obtain the most parsimonious model, which includes only key environmental and trait variables that interact in ant abundance predictions. In addition, the same fourth-corner analyses as described above were conducted on a "common species" dataset, where species occurring in fewer than 5% of sites were excluded.

Results

Ant species richness, abundance, and co-occurrence: A total of 6641 individual ants, belonging to 39 species from 18 genera, were collected across all sites (n = 168). Ant species richness, based on rarefied numbers of individuals (n = 428) was highest in habitats with three vegetation layers (trees, shrubs and herbs) (n = 28), followed by habitats with two layers (trees and herbs) (n = 24) and lastly habitats with one vegetation layer (herbs) (n = 16) (Fig 2A). Ant diversity, measured as Simpson's inverse (1 / D), was higher in habitats with three vegetation layers (1 / D = 12.9), than in habitats with two (1 / D = 12.4) or one vegetation layer (1 / D = 7.6). Adequacy of sampling was high (88 - 98%) across the three habitat types, as shown by the asymptotic behaviour of species accumulation curves (Fig. 2B), indicating that an appropriate proportion of the local species pool, that is, meat-attracted ants within the predator and scavenger guilds, had been collected.

Overall, the most numerically dominant genera were *Iridomyrmex*, *Pheidole*, and *Rhytidoponera*, occurring in 32%, 15% and 12% of the samples; all other genera were found in less than 10% of samples. In woody and more complex habitats *Iridomyrmex* was dominant, followed by *Rhytidoponera* and *Anonychomyrma*, whereas in habitats with only one vegetation layer (herbs), *Pheidole* was the dominant genus, followed by *Iridomyrmex* and *Nylanderia*. Dominant species – in both abundance and frequency – were *Iridomyrmex* near *septentrionalis* and *Iridomyrmex sucheri*, followed by *Anonychomyrma* sp. 1 (*nitidiceps* group) (abundance), *Rhytidoponera victoriae* (frequency of occurence), and *Crematogaster laeviceps* (Fig. S1, Tab. S1, as digital supplementary material to this article, at the journal's web pages).

A third of the ant species (n = 13; 33%) were collected from only one habitat type, of which 7 species were unique to the high complexity habitat. These included *Ochetellus* sp. 1, *Meranoplus minor* and *Froggattella kirbii*. A total of 28% (n = 11) of ant species were collected from all

three habitat types, including the three most dominant species described above and four species within the genus *Pheidole*. Similarly, 28% (n = 11) of species co-occurred in the two woody habitat types, which included *Crematogaster laeviceps*, *Anonychomyrma* sp. 1 (*nitidiceps* group) and three species within the genus *Iridomyrmex*. Only three species (8%) co-occurred on low and medium complexity habitats (*Nylanderia nana*, *Cardiocondyla nuda* and *Pheidole* sp. 9 (*ampla* group)) and one (*Pheidole* sp. 3 (Group E)) on low and high complexity habitats.

Species traits: Each of the four ant traits was significantly associated with a different habitat complexity variable. Overall, ant size (measured as WL) ranged from 0.49-2.35 mm. WL was positively associated with tree density (*Wald* χ^2 = 13.742, P = 0.0002; Df 464,1; Fig. 3A; Table 1A) and all other variables were not significant. CI ranged from 82-107 and showed a positive relationship with tree biomass (*Wald* χ^2 = 9.2341, P = 0.0023; Df 464,1; Fig. 3B; Table 1B), while no other variables were significant. RFL ranged from 0.66-1.09 and was positively associated with shrub density (*Wald* χ^2 = 7.0761, P = 0.008; Df 464,1; Fig. 3C; Table 1C). However, Fig. 3C shows that this trend is weak, and the confidence intervals of the model output are large. RSL ranged from 0.58-0.98 and was positively associated with herb cover (*Wald* χ^2 = 6.6678, P = 0.010; Df 464,1; Fig. 3D; Table 1D) and shrub density (*Wald* χ^2 = 5.9508, P = 0.014; Df 464,1; Fig. 3D insert; Table 1D).

Ant assemblage composition: Ant species composition differed significantly among sites (*Wald* χ^2 = 33.473, P = 0.001; Df 146,1). The most parsimonious model, based on ΔAIC = 110, included three of the six habitat variables. Species composition was significantly associated with tree biomass (*Wald* χ^2 = 10.737, P = 0.002) and tree density (*Wald* χ^2 = 7.115, P = 0.04) but not with herb cover (*Wald* χ^2 = 6.981, P = 0.08). Differences in species composition were largely driven by significantly higher occurrences of *Crematogaster laeviceps*, *Notoncus* sp. 1 (*enormis* group) and *Rhytidoponera victoriae* at sites with trees and shrubs; *Anonychomyrma* sp. 1 (*nitidiceps* group) and *Iridomyrmex* near *septentrionalis* were more frequent at sites with herb and tree layer, while *Pheidole* sp. 5 (*tasmaniensis* group), *Pheidole* sp. 2 (*pyriformis* group) and *Nylanderia rosae* occurred significantly more frequently at sites with only a herb layer (Tab. S1).

Assemblage trait structure: Overall, the fourth-corner analyses revealed significant assemblage level species trait-environment interactions (*Wald* χ^2 = 7.074, P = 0.001; Fig. 4), indicating that these traits explain a significant amount of the variation in species responses. The relationships here may be different from those seen at the individual species trait level (Fig. 3), as the fourth-corner analyses consider the ant assemblage as a whole. WL showed a strong positive relationship with tree density and a weaker one with shrub biomass, indicating that larger ants are dominant in assemblages in woody habitats. RFL showed a slight negative association with shrub biomass and tree density, suggesting that some of the predominant ants in woody habitats have relatively shorter legs. RSL was negatively related to shrub biomass and had a strong positive relationship with herb cover, suggesting that ants with shorter antennae were frequent in shrubby environments, whereas ants with long antennae prevailed in habitats with a dense herb (grass) layer. CI (HW / HL) was positively associated with tree biomass, shrub density and herb height, indicating that broad-headed ants were prevalent in complex habitats with high herbs and grasses, large trees and many shrubs.

The fourth-corner analyses of the common species dataset (n = 17 species occurring at > 5% of the sites) also showed significant interactions between species traits and environmental habitat variables (*Wald* χ^2 = 7.808, P = 0.001; Fig. S2). Similar relationships, but fewer in total than those described above were found: WL was positively related to tree density. RSL was strongly negatively associated with shrub biomass and positively with herb cover, and CI was positively related to tree biomass.

Discussion

We used ant assemblages collected from three different habitat types on urban golf courses to assess whether there is an association between habitat complexity and ant species richness, species composition and functional trait variation. More complex habitats consisting of three vegetation layers – trees, shrubs and herbs – harboured more species than simpler ones. Our single species trait analyses showed associations of each trait with a different environmental complexity variable. This finding was corroborated by our fourth-corner analysis that considers the overall assemblage of traits and species.

Complex habitats harbour more species: As expected, ant species richness was positively related to habitat complexity. The habitat type with three vegetation layers harboured twice as many ant species as the single-layer habitat (lacking trees and shrubs). This supports the "habitat heterogeneity hypothesis" (MacArthur & MacArthur 1961, MacArthur & Wilson 1967), which predicts that the higher complexity of habitats with three vegetation layers – trees, shrubs and herbs – should provide more nesting and foraging sites and a greater food supply. Our results are in line with previous findings in South Australia where twice as many ant species were found in woodland sites as in heath sites (Andersen 1986). In contrast, studies on Sydney sandstone ridgetop woodlands (Lassau & Hochuli 2004) and in urban green spaces in Melbourne (Ossola & al. 2015), found higher ant species richness in low complexity habitats. Differences in findings between studies might derive from different measures of habitat complexity, as the latter two studies took additional measures into account, such as litter ground cover and volume of understorey vegetation (Ossola & al. 2015) or ground cover by rocks, logs and debris (Lassau & Hochuli 2004).

Larger ants in woody habitats, and longer antennae in dense herb cover: Each of the four tested species traits was associated with a different environmental complexity variable (Fig. 3). The strongest associations

were between WL and tree density (positive), CI and tree biomass (positive), and RSL and herb cover (positive) and shrub density (negative). This shows that in woody habitats, ants tended to be larger and have wider heads. Antennal scape length defines the radius around an ant's head in which it can perceive chemosensory and tactile information. It is therefore closely related to sensory abilities, such that longer scapes might enable the easier following of pheromone trails. Ants living in an environment with dense groundcover might rely heavily on chemical cues to successfully find their way between food and nest.

Assemblage-level patterns (fourth corner): The fourth-corner analyses revealed assemblage-level relationships between functional ant traits and environmental habitat variables. While the results are more nuanced, the overall pattern is very similar to our single trait analysis discussed above. The only noticeable difference is an increased negative association of RSL with shrub biomass, rather than shrub density (Fig. 4). The strongest relationship was between body size (measured as WL) and tree density (Fig. 4). This might reflect the higher frequency of larger ants (e.g., *Rhytidoponera victoriae*, *Notoncus* sp. 1 (*enormis* group) and *Iridomyrmex sucheri*) in wooded habitats. Our finding contrasts with a range of other studies, which found larger ants to be more abundant in more open, less complex habitat types in south-east Australia (Yates & al. 2014, Gibb & al. 2015), in South Africa (Gibb & Parr 2010), and after vegetation removal by burning in northeast Spain (Arnan & al. 2013). Other authors could not identify any relationships between body size and habitat complexity variables in urban green spaces (Ossola & al. 2015) or with ground cover complexity (Wiescher & al. 2012). The overall picture is still far from clear, as inconsistent results between studies might also arise due to variations in accounting for habitat complexity. In addition, we found that ant species with higher RSL prevailed in habitats with high herb cover. This assemblage level trait-environment relationship closely matches the single trait relationship. This might reflect the predominance of *Pheidole* spp., *Nylanderia rosae* and *N. nana* in the assemblages on fairways. Lastly, we found that ant assemblages in habitats with high tree and herb biomass had more species with broader heads (higher CI). This might result from a greater abundance of *Anonychomyrma* sp. 1 (*nitidiceps* group), *Crematogaster laeviceps* and *Iridomyrmex* near *septentrionalis* in the assemblages. This contrasts with the prevalence of broad-headed species at sites with little shrub cover and woody debris ground cover in south-east Australia (Gibb & al. 2015).

The size-grain hypothesis: Our findings do not support the size-grain hypothesis, according to which more complex habitats (with more rugose surfaces and smaller interstitial openings) should influence some functional traits in ants (Kaspari & Weiser 1999). Following this hypothesis, we would have expected to find smaller body size, relatively shorter legs and narrower heads in high-complexity habitats (Kaspari & Weiser 1999, Sarty & al. 2006, Gibb & Parr 2010). However, our habitat complexity measures might be on a different scale to those considered in the hypothesis. Our measurements attempt to capture the structural complexity of all vegetation layers, from the size and density of tree trunks to the percentage of herb cover. The proposed effect of the size-grain hypothesis should be most noticeable on the smallest of scales, where the size of the interstitial spaces matches more or less the size of ants.

Limitations: There are some caveats associated with this study, which might limit the generalisability of our findings. First, ant surveys were only conducted once; repeat surveys in the following year or throughout the same season would have yielded more ants. Second, the sampling approach focused on daylight active ants that scavenge or actively predate on invertebrates. Deploying another sugar-based bait would have widened the targeted ant fauna. However, many ants are opportunistic generalist feeders gathering many different food types, and the protein and fat of our food baits would have been attractive to most species. Using baits in Eppendorf tubes may have shifted the focus towards collecting smaller sized ants, but this influence might be marginal as our samples did in fact contain a large proportion of large ants, including species of *Rhytidoponera*, *Iridomyrmex*, *Aphaenogaster* and *Notoncus*.

Conclusions: Our results show that habitat complexity affects ant assemblages. The ant fauna in simpler habitats has fewer species and exhibits a different suite of functional traits to those in more complex habitats. Complex habitats consisting of three vegetation layers harboured consistently more species, thereby supporting the "habitat heterogeneity" hypothesis. Species traits are closely related to environmental complexity variables. Ant assemblages in tree-rich habitats predominantly consist of larger species with broader heads. Smaller ant species with longer antenna scapes prevailed in treeless habitats with dense herb cover. Our study suggests that habitat complexity can act as an environmental filter in driving species diversity and functional traits of ant assemblages. Our results can be used to infer potential turnover in ant assemblages due to habitat changes, such as shrub and tree clearing and the general simplification of habitats.

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