

The ants of Talaroo Station: diversity, composition and habitat associations of a tropical savanna insect assemblage

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Abstract

The rich diversity of ants in the tropical savannas of northern Australia has been sampled extensively in the Northern Territory and Western Australia, but rarely in Queensland. We present a survey of the ants of Talaroo Station in the Einasleigh Uplands, north Queensland, Australia, with 24 sites sampled across a range of habitats, and explore the relationship between assemblage composition and habitat. One hundred and thirty-three ant species were recorded representing 24 genera, six sub-families and seven functional groups. Five genera contributed 83% of all records. Two non-native species, while recorded, were uncommon. Assemblage composition was related to land zone, but aligned more strongly with vegetation along a soil gradient that may reflect moisture-holding capacity and fertility. There was a negative spatial relationship between Dominant Dolichoderinae and non-dominant Opportunists. In its generic and functional group composition, the ant fauna of Talaroo is similar to that of other northern Australian savannas. We suggest that: vegetation at local scales reflects subtleties of soil properties that underlying geology does not adequately encapsulate; ants respond to the same edaphic features as vegetation; and vegetation mapping that hierarchically reflects land zone above floristics has limited value for explaining ant community composition.

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Introduction

Ants are a prominent feature of tropical savanna landscapes (Campos *et al.* 2011) and play a substantial role in ecosystem biomass and energy flows. Their contribution to ecosystem processes has been little studied in north Australian savannas except their role as major predators and/or dispersers of grass and eucalypt seeds (e.g. Watkinsinon *et al.* 1989; Gross *et al.* 1991; Setterfield & Andersen 2018). The north Australian savanna ant fauna is estimated to comprise more than

1,500 species, with very high levels of endemism and 901 species in the monsoonal portion of the Northern Territory alone (Andersen 2000; Andersen *et al.* 2018). Richness of more than 100 species per ha is maintained along a rainfall gradient from the north coast inland to the fringe of the central Australian arid zone (Andersen *et al.* 2015). However, surveys and studies of this fauna have mostly been limited to the Top End of the Northern Territory and, to a lesser extent, the

Kimberley region of Western Australia. Surveys in Queensland's tropical savannas have been conducted at Lawn Hill and Mount Isa in the far west (Andersen 1993; Hoffmann *et al.* 2000) and Mount Carbine in the far east (van Ingen *et al.* 2008).

Based on responses to environmental stress and disturbance, seven functional groups are recognised among ant fauna (Andersen 1995). The north Australian savanna fauna is dominated by highly abundant and aggressive 'Dominant Dolichoderinae' (mainly in the genus *Iridomyrmex* [tyrant ants, meat ants]), and includes numerous species of sub-dominant 'Generalised Myrmicinae' (especially species of *Monomorium* [mono ants] and *Pheidole* [big-headed ants]) and 'Hot-Climature Specialists' (particularly *Melophorus* [furnace ants] and *Meranoplus* [shield ants] species) (Andersen 2000; Andersen *et al.* 2015). 'Opportunists' (notably *Rhytidoponera* species [pony ants]) predominate at environmentally stressed sites with low ant diversity and commonly where there are few Dominant Dolichoderinae (Hoffmann & Andersen 2003). The arid-adapted nature of the fauna renders it highly resilient to dry-season fires that are frequent in parts of northern Australia (Andersen *et al.* 2014; Vasconcelos *et al.* 2017). The ant fauna is also generally resilient to moderate intensities of grazing, being more strongly structured by variation in soil and vegetation type (Hoffmann 2010; Arcoverde *et al.* 2017; see also Andersen *et al.* 2015; Cross *et al.* 2016). Ant assemblages in Brazilian savanna are similarly structured substantially by soil and vegetation type (Silva *et al.* 2017) and relatively resistant to grazing but not land clearing (Dalle Laste *et al.* 2019).

Here we describe assemblage and functional group composition and species richness, along with their environmental correlates, of the ant fauna of Talaroo Station in the Einasleigh Uplands in north Queensland. We consider the extent to which these patterns are similar to those identified elsewhere in the Australian tropical savannas. We also evaluate the relative merits of land zone (surface geology) and vegetation type in describing these patterns, considering that vegetation types in the Einasleigh Uplands often show only limited correspondence with land zones (DC Franklin, personal observation).

Methods

Study area

Talaroo Station (18°05'S, 143°52'E), located between Georgetown and Mount Surprise in Queensland's Einasleigh Uplands bioregion, is a 31,500 hectare pastoral lease now de-stocked and run by the Ewamian Aboriginal Corporation. In 2014 it was formally declared a nature refuge under the *Nature Conservation Act 1992*. It comprises a 28 km frontage to the Einasleigh River with associated riparian vegetation, an undulating plain supporting woodland and open woodland (mostly eucalypt-dominated) on metamorphic, sandsheet and granitic substrates and an elevated rhyolitic and granitic portion (part of the Newcastle Range) that supports low open eucalypt woodlands and *Acacia* and *Cochlospermum* shrublands. The property ranges from 340 to 500 m above sea level and has a mean annual rainfall of c. 700 mm with a high level of variability between years.

Field methods

Ants were surveyed at 24 sites selected as representative of the diversity of land zones, vegetation types and disturbance histories present on the station (Table 1). In general, two sites were selected for each major vegetation type/land zone combination (see *Data analysis*). Members of each pair were placed as far apart from each other – and interspersed with other combinations – as permitted by landscape and access considerations. Three sites had been burnt early in the dry season of the study (C, Q, R) and one in 2015 (K), the others being unburnt since at least 2012 (<https://www.firenorth.org.au/nafi3/>, viewed 2 Oct. 2017).

Ants were sampled using pitfall traps over the four days 2 to 5 Oct. 2017. Weather during this period was hot with daily minimums of c. 21 °C and maximums of c. 38 °C. Six millimetres of rain was recorded at the station homestead on the afternoon of 2 Oct. 2017, falling on some sites only and is thought unlikely to have affected results (Alan Anderson, personal communication). Each site was sampled using a 5 x 3 grid of traps with 10 metre spacing, set for 48 hours. Traps were plastic containers (45 mm in diameter and 55 mm deep) that were half-filled with 50 % ethylene glycol solution and buried with their rims flush to the ground surface.

Table 1. Environmental attributes used in analysis of 24 sites surveyed for ants at Talaroo Station, October 2017.See *Data analysis* for details of land zones and vegetation types.

Site	Land zone	Vegetation type	Herb cover (% class)
A	igneous (granite)	<i>Acacia</i> shrubland	>75 %
B	igneous (granite)	ironbark woodland	>75 %
C	alluvial	box woodland	50–75 %
D	alluvial	box woodland	>75 %
E	metamorphic	box woodland	>75 %
F	metamorphic	box woodland	>75 %
G	alluvial	riparian	10–25 %
H	alluvial	riparian	10–25 %
I	alluvial	natural grassland	>75 %
J	alluvial	natural grassland	>75 %
K	colluvial	ironbark woodland	>75 %
L	colluvial	box woodland	50–75 %
M	spring	tea-tree swamp forest	>75 %
N	spring	tea-tree swamp forest	>75 %
O	igneous (rhyolite)	<i>Acacia</i> shrubland	>75 %
P	igneous (rhyolite)	<i>Acacia</i> shrubland	10–25 %
Q	igneous (granite)	ironbark woodland	5–10 %
R	igneous (granite)	ironbark woodland	25–50 %
S	igneous (rhyolite)	<i>Acacia</i> shrubland	>75 %
T	igneous (rhyolite)	<i>Acacia</i> shrubland	>75 %
U	alluvial	cleared grassland	>75 %
V	alluvial	cleared grassland	>75 %
W	igneous (granite)	ironbark woodland	>75 %
X	metamorphic	ironbark woodland	>75 %

At each site, we recorded the cover class of woody plant species, and of herbs (graminoids and forbs), in a 50 x 50 metre plot centred on the pitfall array, all in the period 28 to 31 August 2017. Cover classes were estimated in categories of 0, <1, 1–5, 5–10, 10–25, 25–50, 50–75 and >75 %. In addition, notes were taken on vegetation structure, the nature and state of the ground layer, surface soil type, rock type, slope, termite mounds, heterogeneity and evidence of disturbance.

Data analysis

Ants were sorted to species and, where possible, named by reference to the ant collection held at Darwin's CSIRO Tropical Ecosystems Research Centre – the largest and most comprehensive collection of northern Australian ants. However, as

a large majority of ant species in northern Australia are undescribed (Andersen 2000), taxa were attributed to species groups following Andersen (2000) or assigned codes that relate to this study only (Table S1). Species were then classified into functional groups (Table S1) in relation to environmental stress and disturbance following Andersen (1995). Common names for native ants follow Andersen (2002).

The primary metric employed in this study is frequency of occurrence (FoO), namely the number of traps in which the species was detected for each site. From this we derived *summed frequencies of occurrence* (summed FoO), which are the sum of species FoOs for each of sub-family, genus and functional group, providing a combined measure of commonness with one of species richness.

Three environmental metrics that describe alternative perspectives on site attributes (land zone, vegetation type and grass cover class) were used in our appraisal of ant–habitat relationships. Land zones generally follow the classification underlying Queensland Regional Ecosystem (RE) mapping (DEHP 2016; Wilson & Taylor 2012), interpreted from field observations and a combination of RE and surface geology mapping available through Queensland Globe (SoQ 2018). We note two exceptions: we have treated wooded swamp vegetation associated with a thermal spring as a

distinct land zone, and for graphic purposes but not statistical analysis we recognise two sub-types of the igneous land zone, granite and rhyolite, as these are distinct in the field. Vegetation was classified into seven categories (Table 2) based on our extensive prior knowledge of the station; ant survey sites were then categorised by vegetation type based on the observed woody plant composition. Though there are some strong associations between land zone and vegetation type, there is also substantial uncoupling of these (e.g. ironbark woodland on colluvial, igneous and

Table 2. Seven vegetation types used to analyse ant–habitat relationships at Talaroo Station. These are illustrated in Figs. S1-7 (Supplementary file).

Short title	Descriptive notes	Land zone and other notes
cleared grassland	dense annual and perennial grasses	alluvial with cracking black clays; has history of intense grazing
natural grassland	annual grasses; few woody plants including the small tree <i>Atalaya hemiglauca</i> (Whitewood) and the shrub <i>Carissa spinarum</i> (Conkerberry)	alluvial; prone to inundation or waterlogging, with a shallow, impermeable B-horizon
riparian	open woodland to open forest of <i>Eucalyptus camaldulensis</i> (River Red Gum) and/or <i>Melaleuca leucadendra</i> / <i>argentea</i> / <i>fluviatilis</i> (broad-leaved paperbarks)	alluvial; loose sand in stream beds, well consolidated clay loams on banks
tea-tree swamp forest	<i>M. bracteata</i> (Black Tea-tree) forest	interpreted as alluvial, associated with overflow of thermal spring
ironbark woodland	<i>E. crebra</i> / <i>cullenii</i> / <i>melanophloia</i> (ironbarks) with <i>Corymbia erythrophloia</i> complex (red bloodwoods)	on well-drained metamorphics, granite and colluvial soils; united across ironbark species by a well-developed tussock grass layer and a moderate shrubby understorey of <i>Gardenia vilhelmii</i> (Breadfruit) and <i>Petalostigma</i> spp. (quinine trees)
box woodland	variously dominated by <i>E. microneura</i> (Georgetown Box, drier sites), <i>E. leptophleba</i> (Molloy Red Box) and/or <i>C. polycarpa</i> (Long-fruited Bloodwood), often with <i>Terminalia platyptera</i> (Wing-fruited Terminalia) on drier sites	variously on alluvial, colluvial or metamorphic soils; typically with low sparse annual grasses and few shrubs, but grades into the understorey typical of ironbark woodland especially on metamorphic soils.
<i>Acacia</i> shrubland	<i>Acacia julifera</i> , <i>A. monticola</i> and/or other <i>Acacia</i> species, with a low to moderate density of small (6–12 m), emergent eucalypts (<i>E. microneura</i> , <i>E. shirleyi</i> [Shirley's Ironbark], <i>C. erythrophloia</i> complex)	on elevated site with skeletal soils in the Newcastle Range, mostly on rhyolite but also more elevated granite

metamorphic land zones) (Table 1), at least some of which is related to soil texture and, in the case of alluvial sites, to seasonal inundation, flood turbulence and waterlogging, and their interaction with soils.

To evaluate the relative similarity of the ant assemblage across sites, species composition was compared in multi-dimensional space using the Bray-Curtis similarity measure applied to frequency of occurrence of species, and species richness compared using the Euclidean distance measure. To evaluate the relationship between ant assemblages and habitat, these response variables were then tested individually for relationships with land zone, vegetation type and herb cover class (treated as a categorical variable but not for species richness) using permutational ANOVAs with 9999 permutations in the PERMANOVA add-on (Anderson *et al.* 2008) to PRIMER v6 (Clarke & Warwick 2001; Clarke & Gorley 2006). This suite of analytical tools allows both multivariate response variables (species composition) and univariate response variables (species richness) to be associated with categorical variables, with probabilities calculated by permutation and thus independently of assumptions of normality and homoscedacity. Herb cover was evaluated as a possible predictor of species richness using a Spearman's rank correlation test.

As vegetation type proved by far the best predictor of species composition in the above analyses, we then evaluated the role of individual ant species in determining community-wide associations with vegetation using the SIMPER module in PRIMER v6. This module evaluates the contributions to Bray-Curtis similarity of species to pair-wise site similarities. Further, we evaluated vegetation as a predictor of summed frequency of occurrence of each functional group (a measure of abundance), and also of summed frequency of occurrence (a measure of relative abundance) standardised so that site totals sum to 100%. Tests were permutational ANOVAs (described above) using the Euclidean similarity measure.

Results

Faunal overview

One hundred and thirty-three ant species were identified, belonging to 24 genera, six sub-families and seven functional groups (Tables 3, S1). The richest genera were *Monomorium* (26 species) and

Melophorus (furnace ants, 19 species). Two introduced species (*Paratrechina longicornis* – the Longhorn or Black Crazy Ant, and *Tetramorium simillimum*) were recorded in a total of nine pitfalls and four sites, with *P. longicornis* present in only seven pitfalls at the two tea-tree swamp forest sites.

Iridomyrmex was by far the most frequently recorded genus as measured by FoO, followed by *Melophorus*, *Monomorium*, *Rhytidoponera* and *Pheidole* (big-headed ants) (Table 3), and together these contributed 83% of all species records. The most frequently recorded species were *Iridomyrmex* sp. 1 (*anceps* gp., Tropical Tyrant Ant; collected in 157 traps at 19 sites), *I. sanguineus* (Northern Meat Ant, 96, 18), *Monomorium* sp. N2 (*nigrius* gp., Black Mono Ant; 51, 15), *Rhytidoponera* sp. A1 (*aurata* gp., Lesser-horned Pony Ants; 47, 13), *Melophorus* sp. A1 (*aeneovirens* gp., Giant Beaked Furnace Ants; 42, 18), *Iridomyrmex* sp. D (40, 12) and *Rhytidoponera* nr. *rufithorax* (40, 10). Together these seven (5%) species contributed 40% of all records. The most frequently recorded functional groups were Dominant Dolichoderinae, Generalised Myrmicinae, Hot-Climate Specialists and Opportunists, which together contributed 94% of all records (Table 3). Cryptic species, Specialist Predators and Subordinate Camponotini were scarce. High frequency generally corresponded with high species richness, the notable exception being that Dominant Dolichoderinae (and, correspondingly, sub-family Dolichoderinae and genus *Iridomyrmex*) were frequent but relatively species-poor, whilst the opportunist genus *Tetramorium* (pennant ants, Opportunists) were infrequent but relatively diverse.

Forty-four species were collected in only a single trap, and a further twelve species at only one site. The species accumulation curve shows that 24 sites were not enough to fully sample Talaroo's species richness (Fig. 1). Estimates of the number of species likely to be encountered with infinite sampling ranged from 156 (bootstrap estimator) to 209 (jackknife2 estimator).

Variation among sites

Six to 35 species were recorded per site (mean 19.3) (Fig. 2). The three richest sites, D, L and Q, were on different land zones (alluvial, colluvial, igneous [granite] respectively), although all

Table 3. Species richness and summed Frequencies of Occurrence (summed FoO) of ant sub-families, most speciose genera and functional groups collected in pitfall traps at 24 sites on Talaroo Station, North Queensland, October 2017.

A full list of species with their functional groups and FoO at each site, is provided in Table S1.

Taxon/Functional Group	No. (%) of species	summed FoO (%)	No. (%) of sites
<i>Sub-family</i>			
Dorylinae	1 (0.8)	2 (0.2)	2 (8.3)
Ponerinae	5 (3.8)	28 (2.3)	15 (62.5)
Ectatomminae	11 (8.3)	143 (12.0)	20 (83.3)
Myrmicinae	63 (47.4)	384 (32.2)	24 (100)
Dolichoderinae	15 (11.3)	369 (30.9)	24 (100)
Formicinae	38 (28.6)	267 (22.4)	23 (95.8)
<i>Most speciose genera (>10 species)</i>			
<i>Monomorium</i> (Myrmicinae, Generalised Myrmicinae and Hot-Climature Specialists)	26 (19.5)	170 (14.2)	22 (91.7)
<i>Melophorus</i> (Formicinae, Hot-Climature Specialists)	19 (14.3)	193 (16.2)	21 (87.5)
<i>Iridomyrmex</i> (Dolichoderinae, Dominant Dolichoderinae)	12 (9.0)	355 (29.8)	23 (95.8)
<i>Pheidole</i> (Myrmicinae, Generalised Myrmicinae)	12 (9.0)	134 (11.2)	20 (83.3)
<i>Rhytidoponera</i> (Ectatomminae, Opportunists)	11 (8.3)	143 (12.0)	20 (83.3)
<i>Tetramorium</i> (Myrmicinae, Opportunists)	11 (8.3)	22 (1.8)	14 (58.3)
<i>Functional group</i>			
Dominant Dolichoderinae	13 (9.8)	360 (30.2)	23 (95.8)
Subordinate Camponotini	15 (11.3)	47 (3.9)	13 (54.2)
Hot-Climature Specialists	36 (27.1)	247 (20.7)	22 (91.7)
Cryptic species	2 (1.5)	6 (0.5)	4 (16.7)
Opportunists	31 (23.3)	233 (19.5)	23 (95.8)
Generalised Myrmicinae	31 (23.3)	280 (23.5)	24 (100)
Specialist Predator	5 (3.8)	20 (1.7)	14 (58.3)
Total	133 (100)	1,193 (100)	24 (100)

supported woodland (2 x box, 1 x ironbark). Site O (igneous [rhyolite], *Acacia* shrubland) had exceptionally low species richness and capture rates, but its ecologically paired site (P) had close to average values for both variables. Site H had low richness but unusually high capture rates, but its paired site (G) was again middling. We are unaware of any methodological causes for these disparate results, so have retained them in analyses. Species richness did not vary significantly with either land zone or vegetation type (Table 4), nor with grass cover (Spearman's $R = -0.17$, $n = 24$, $P = 0.43$). The three sites burnt in the year of study were among the richest sites (Fig. 2), but there is

insufficient data to further evaluate fire associations.

Species composition was strongly related to land zone and even more strongly to vegetation type (Table 4, Fig. 3) notwithstanding the weakening effect of two of the outliers (J, O) on the analyses. The ordination shows a gradient from more fertile and moisture-retentive sites (left) to upland sites with skeletal soils (right) (particularly evident in Fig. 3B). Post hoc analysis ($P < 0.05$) revealed that land zone distinctions were driven primarily by the difference between alluvial and igneous sites and between spring and igneous sites. Although not

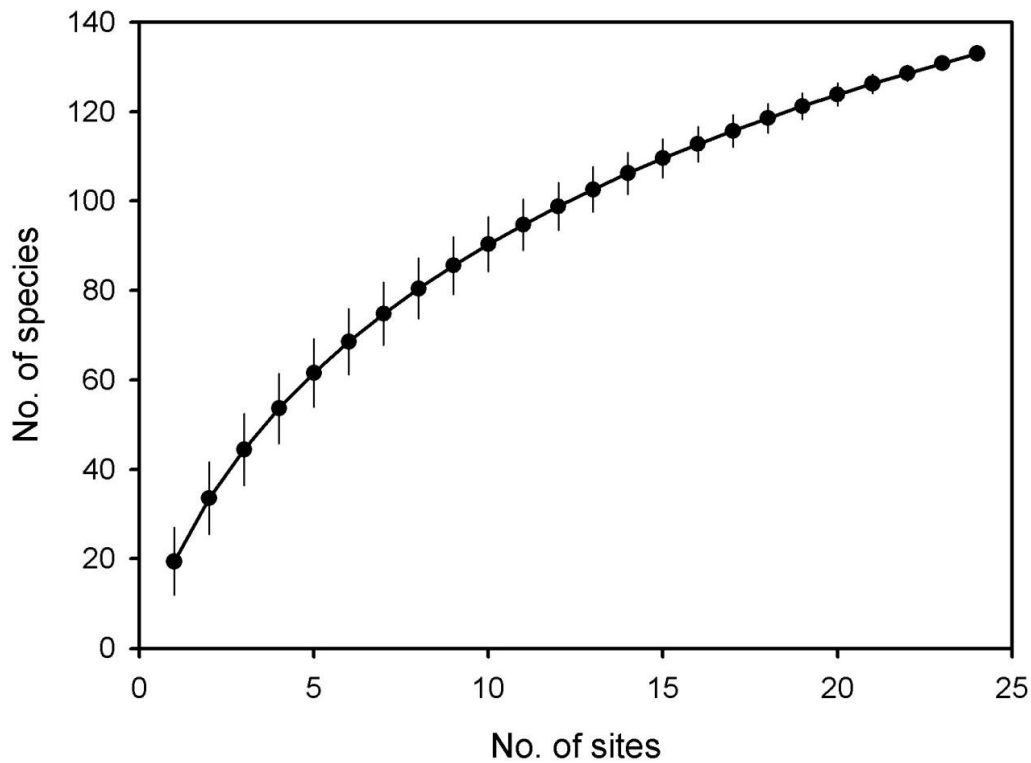


Figure 1. Species richness accumulation with increased number of sites (mean \pm s.d. from 9999 permutations) sampled at Talaroo Station.

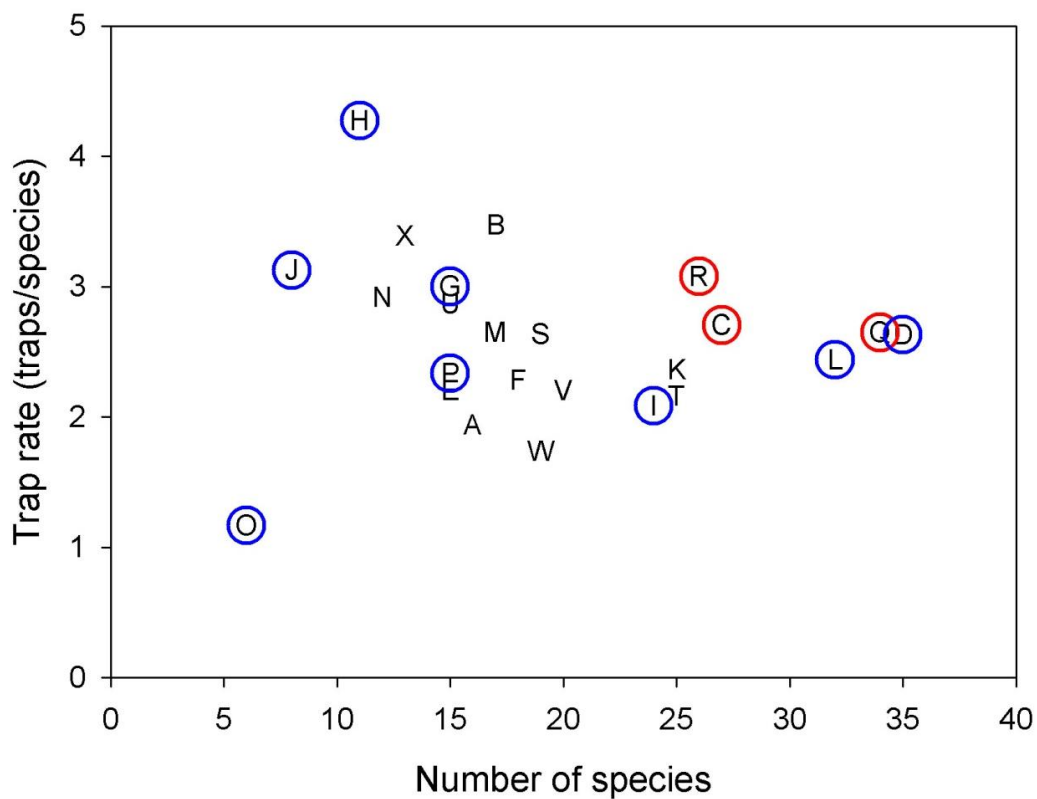


Figure 2. Site richness and trap rates for 24 ant survey sites at Talaroo Station, October 2017. Trap rates averaged across species. Sites burnt in the 2017 dry season prior to survey are circled in red and additional sites named in the text are circled in blue.

Table 4. Summary of permutational ANOVAs of relationships between environmental variables and ant composition and species richness across 24 sites at Talaroo Station.

Probabilities significant at $P < 0.05$ are emboldened.

Response variable	Predictor variable	d.f.	P
Species richness	Land zone	4,19	0.38
	Vegetation type	6,17	0.30
Species composition	Land zone	4,19	0.004
	Vegetation type	6,17	<0.0001
	Herb cover	4,19	0.83

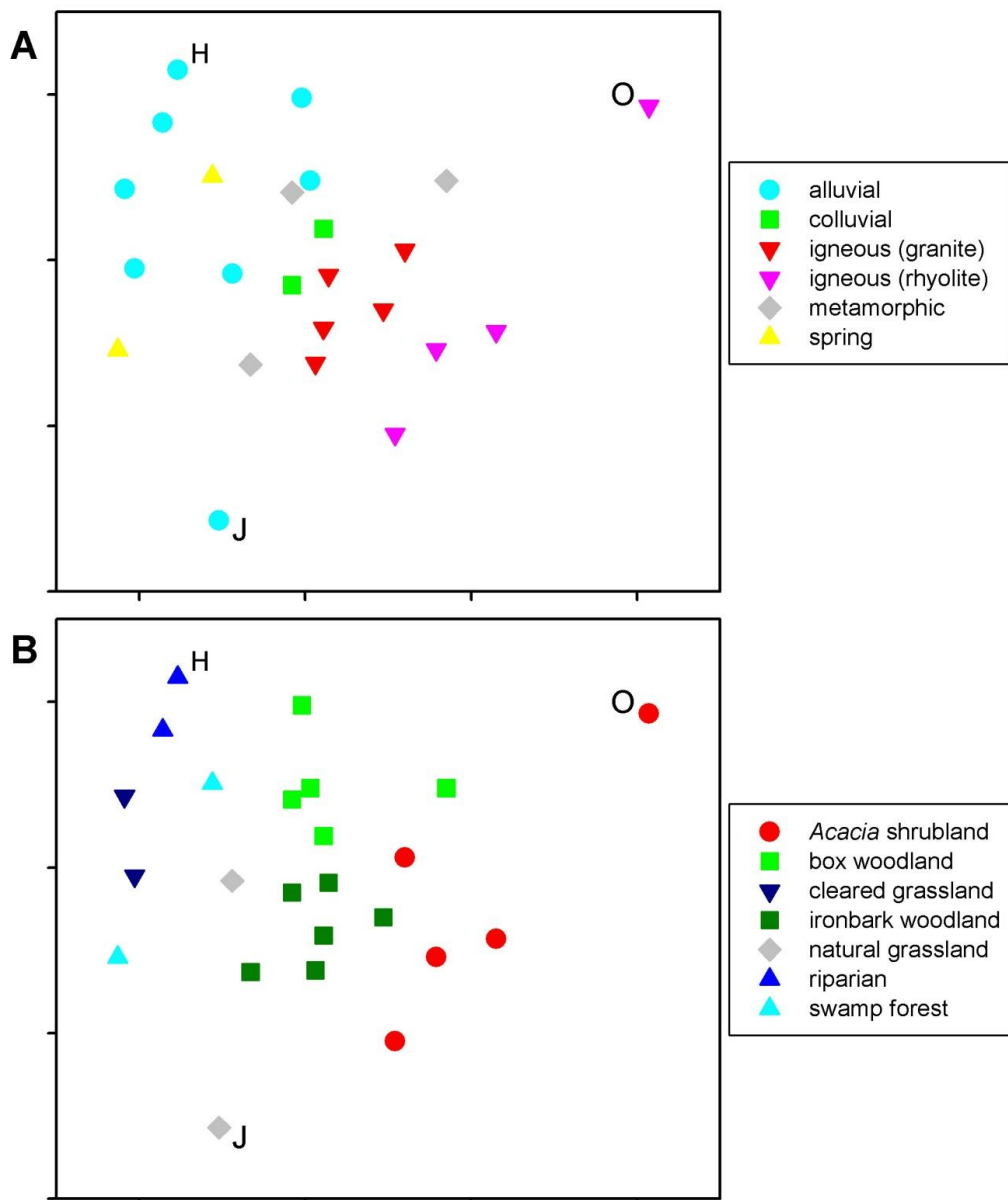


Figure 3. NMDS ordination of sites according to ant species composition, illustrating the effects of Land zone (A) and vegetation type (B). The three sites (H, J, O) identified as outliers in analysis of species richness and capture rates (Fig. 2) are labelled.

incorporated into statistical analysis, igneous (granite) and igneous (rhyolite) sites also showed clear differentiation in their species composition. Post hoc analysis of vegetation types revealed numerous significant pair-wise differences, but failed to discriminate between alluvial, tea tree

swamp forest, natural grassland and cleared grassland sites.

The twelve most discriminating species in the analyses of vegetation type in Table 4 and Fig. 3 represented four of seven functional groups (Table 5A). The seven species that characterised four or

Table 5. Mean frequency of occurrence by vegetation type of ant species: A. that contributed most to vegetation patterning (Table 4, Fig. 3b) – more than 5.0 average dissimilarity to at least one Bray-Curtis pair-wise comparison of vegetation types; and B. other common species (caught in >20 traps).

n is the number of traps in which the species was recorded. Vegetation types are (in abbreviated form) those in Table 2 and Fig. 3b. Frequency of Occurrence for vegetation types featuring in a pair-wise comparison identified by the 5.0 threshold are highlighted: dark are above mean, pale are below mean. Asterisk indicates non-native species.

Ant species	Functional group	n	Vegetation type							Vegetation pairs discriminated at >5.0 dissimilarity
			A. cleared	B. natural grassland	C. riparian	D. tea-tree	E. ironbark	F. box	G. Acacia	
A. Species contributing most of vegetation patterning of the assemblage										
<i>Iridomyrmex</i> sp. 1	Dom. Dol.	157	7.0	4.5	7.5	9.0	7.2	10.6	1.0	AB,AG,BC,BD,BE,BF,BG,CG,DF,DG,EG,FG
<i>Iridomyrmex sanguineus</i>	Dom. Dol.	96	1.0	4.0	0.0	1.0	10.0	2.8	2.0	AE,BC,BD,BE,BG,EC,EF,EG
<i>Cardiocondyla atalanta</i>	Opportunists	21	0.0	0.0	6.0	3.5	0.0	0.2	0.2	AC,BC,CE,CF,CG,DE,DG
<i>Iridomyrmex septentrionalis</i>	Dom. Dol.	19	9.0	0.5	0.0	0.0	0.0	0.0	0.0	AB,AC,AD,AE,AF,AG
<i>Iridomyrmex</i> sp. D	Dom. Dol.	40	0.5	0.5	6.5	1.0	0.5	4.0	0.0	AD,BC,CD,CE,CG
<i>Iridomyrmex</i> sp. B (<i>suchieri</i> gp.)	Dom. Dol.	24	2.5	0.0	6.0	2.5	0.0	0.4	0.0	BC,CE,CF,CG
<i>Rhytidoponera</i> nr. <i>rufithorax</i>	Opportunists	40	0.0	4.5	0.0	2.5	2.8	0.0	1.8	AB,BC,BF,BG
<i>Melophorus</i> sp. F1	Hot-climate	14	4.0	1.0	0.0	0.5	0.2	0.2	0.2	AB,AG
<i>Monomorium</i> sp. N2	Gen. Myrm.	51	0.0	0.0	0.5	0.0	2.0	5.6	2.0	BF,DF
<i>Nylanderia</i> sp. A	Opportunists	17	0.5	0.0	4.0	2.0	0.3	0.4	0.0	CG
* <i>Paratrechina longicornis</i>	Opportunists	7	0.0	0.0	0.0	3.5	0.0	0.0	0.0	DG
<i>Pheidole</i> sp. F	Gen. Myrm.	12	2.5	3.5	0.0	0.0	0.0	0.0	0.0	BG
B. Other common species										
<i>Rhytidoponera</i> sp. A1 (<i>aurata</i> gp.)	Opportunists	47	0.5	0.0	0.0	0.0	4.2	1.6	2.6	
<i>Pheidole</i> sp. C1	Gen. Myrm.	45	1.5	0.0	0.0	1.5	2.7	2.4	2.2	
<i>Melophorus</i> sp. A1	Hot-climate	42	0.5	1.0	0.0	0.5	2.7	2.2	2.2	
<i>Pheidole</i> sp. E	Gen. Myrm.	33	2.0	4.0	0.0	0.0	2.8	0.8	0.0	
<i>Melophorus</i> sp. F2	Hot-climate	32	0.0	1.5	0.0	0.0	3.3	1.6	1.0	
<i>Monomorium</i> sp. R1	Hot-climate	22	2.5	0.5	2.0	0.0	0.0	2.0	0.4	
<i>Melophorus</i> sp. Fi1	Hot-climate	21	0.0	0.5	0.0	0.0	1.5	1.6	0.6	

more vegetation pairs comprised five Dominant Dolichoderinae in the genus *Iridomyrmex* and two Opportunists (*Cardiocondyla atalanta* and *Rhytidoponera* nr. *rufithorax*). However, both within and among functional groups for these species, patterns of vegetation preference were species-specific. A further seven species were recorded in more than 20 traps but did not contribute to discrimination of vegetation types at this level (Table 5B) either because their frequencies were relative consistency between vegetation types or had high levels of variance among sites within vegetation types.

The only functional groups to vary significantly between habitats in their frequency of occurrence were Dominant Dolichoderinae and Opportunists; the latter with standardised data only (Table 6). Dominant Dolichoderinae were present in all habitats (and in 23 of 24 sites, Table 3), but their occurrence was extremely low in *Acacia* shrubland (Fig. 4A). Opportunists were also present in all

Table 6. Probabilities from permutational ANOVAs testing the effect of vegetation type on summed frequency of occurrence (summed FoO), and summed FoO standardised, of ant functional groups at Talaroo.

The degrees of freedom are 6,17 in each test. Probabilities significant at $P < 0.05$ are emboldened. Cryptic species were not tested as they were present at too few sites (Table 3).

Functional group	Summed	
	FoO	Standardised
Dominant		
Dolichoderinae	0.03	0.03^a
Subordinate		
Camponotini	0.10	0.08
Hot-Climate		
Specialists	0.36	0.61
Opportunists	0.34	0.04^b
Generalised		
Myrmicinae	0.43	0.51
Specialist Predators	0.48	0.58

^a *Post hoc* analyses ($P < 0.05$): shrubland \neq cleared, riparian and ironbark woodland vegetation types, and nearly also box woodland ($P = 0.06$)

^b *Post hoc* analyses ($P < 0.05$): shrubland \neq ironbark and box woodland, riparian \neq box woodland, and nearly also ironbark woodland \neq box woodland ($P = 0.056$)

habitats and in 23 of 24 sites, but had most consistently higher frequencies in *Acacia* shrubland (Fig. 4B). The generally-negative relationship between Dominant Dolichoderinae and Opportunists implied in Fig. 4 was only weakly evident across sites using absolute summed FoO ($r = -0.19$, $n = 24$, $P = 0.36$), but more strongly so when standardised data were used ($r = -0.58$, $n = 24$, P not applicable due to autocorrelation).

Discussion

With 133 species and an estimated 156+ species with complete sampling, the ant fauna of Talaroo Station is similarly rich to that documented elsewhere in the tropical savannas of northern Australia (see Andersen 1993, Table 3). In its sub-familial, generic and functional group composition, Talaroo's ant fauna is also broadly similar to that documented elsewhere in northern Australia. The two non-native species recorded were uncommon. *Paratrechina longicornis* is typically widespread around human settlements in northern Australia (Andersen 2000) and was most frequent on Talaroo around the hot springs, an area with a history of disturbance. Low abundance of exotic ants was also found in a study area in the north Kimberley with a history of pastoralism in which just one record of one non-native species (*Trichomyrmex mayri*) was recorded (Cross *et al.* 2016).

Habitat associations

We have identified both strong relationships between habitat and the ant assemblage, but also considerable noise in the relationship. While ant species composition was strongly related to our classification of vegetation, functional group composition was only weakly so, with many patterns of vegetation preference being species-rather than functional group-specific, we were unable to explain variation in species richness among sites (*cf* a north Kimberley site [Cross *et al.* 2016] for a strongly contrasting example), and the negative spatial relationship between Dominant Dolichoderinae and Opportunists was present but rather weak (*cf* very strong at another north Kimberley site [Andersen *et al.* 2010]). It may be noteworthy that the three recently-burnt sites were among the five most species-rich sites, though more structured evidence is needed to evaluate this at Talaroo and several previous studies have found no effect of fire frequency or

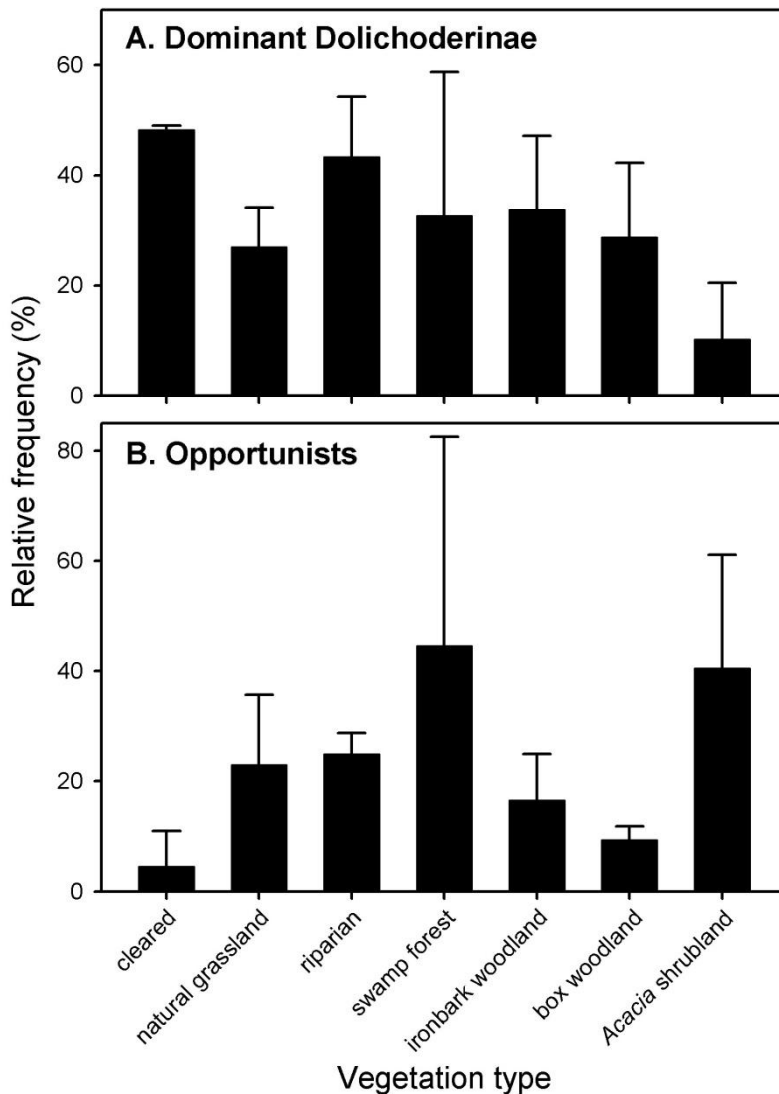


Figure 4. Relative frequency (standardised summed Frequency of Occurrence; mean \pm s.d.) of two ant functional groups across seven habitats at Talaroo Station.

time since fire on ant species richness (Andersen *et al.* 2010; Andersen & Hoffmann 2011). A previous explanation for variation in frequency of Dominant Dolichoderinae (and also Hot-climate Specialists) – i.e. a preference for open sites and tolerance of disturbance in these (Hoffmann & Andersen 2003; Andersen 2019) – is also only equivocally supported by our observations. At Talaroo Station, this functional group was most prevalent in the cleared grassland and well-wooded riparian vegetation (though these may be disturbed by flooding), and not in natural grassland. There was no evidence of preference for particular vegetation types among Hot-climate Specialists. An alternative explanation (Andersen 1995), that environments in which food is scarce (e.g. poorly drained or infertile) disadvantage Dominant Dolichoderinae and favour Opportunists because they are thus not

excluded, seems more plausible, with Opportunists more frequent in the poorly-drained tea tree swamp forest and harsh, rocky upland *Acacia* shrublands.

The strong relationship between habitat and ant assemblage composition demonstrated in Fig. 3, with alluvial sites (riparian, grassland, tea tree swamp forest) grouping to left of the ordinations and igneous sites (especially rocky upland *Acacia* shrubland on rhyolites) to the right, suggests that a key overall correlate of composition is a gradient in soils possibly reflecting fertility and moisture-holding capacity. This gradient was moderately well reflected in the ordination of land zones (surface geology) that underpins Queensland's RE mapping (Wilson & Taylor 2012) (Fig. 3a), but far better reflected in the ordination showing vegetation classes (derived quite independently of

ant composition) (Fig. 3b). The stronger match to vegetation classes arises because ant assemblages were:

- more similar within than between riparian vegetation, cleared grassland and box woodland within the alluvial land zone;
- closely associated within box woodland irrespective of land zone (alluvial, colluvial, metamorphic); and
- closely associated within ironbark woodland irrespective of land zone (colluvial, metamorphic, igneous).

We do not suggest that ant assemblages are structured by trees, but rather that trees reflect soil properties such as fertility and moisture-holding capacity at local scales. In contrast, land zone classifications do so only generically. Variation in ant assemblages between soil types has been demonstrated repeatedly within the Australian tropical savannas (e.g. Andersen *et al.* 2010, 2015; Arcoverde *et al.* 2017) and in savannas overseas (Silva *et al.* 2017), and in may in part be driven by requirements for terrestrial nest sites. The distinction between ant assemblages on rhyolitic and granitic sites (Fig. 3a) further supports a likely role of soils in structuring ant assemblages.

The land zone classification's relatively poor performance in explaining patterns of ant assemblage composition highlights a limit to the application of Queensland RE mapping in some ecological studies, particularly those that reflect local soil properties. Regional Ecosystem mapping is hierarchical, with Queensland first divided into bioregions, then twelve land zones defined by geology and geomorphology, and finally by vegetation structure and floristics (Neldner *et al.* 2017). In the savanna environments of the Einasleigh Uplands at least, the result is frequent repetition of floristically near-identical Regional Ecosystems (REs) across land zones, often in close proximity. On Talaroo, for example, vegetation dominated by *Eucalyptus microneura* occurs on colluvials (RE 9.5.10), metamorphics (RE 9.11.23) and rhyolite (RE 9.12.6) (DEHP 2016), and the species also occurs there on alluvial soils with *E. leptophleba* (personal observations). Analyses of habitat preference at smaller spatial scales needs to reflect on-ground realities at these scales and not be limited to *a priori* vegetation mapping systems which are necessarily broad-brush and hierarchical.

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Supplementary file

A supplementary pdf file accompanies this paper on its web-page. It contains:

- Figs. S1-S7: photos of vegetation types used in this study; and
- Table S1: ant species detected in this study with their functional group and capture rates.

References

- Andersen AN. 1993. Ant communities in the Gulf region of Australia's semi-arid tropics: species composition, patterns of organization, and biogeography. *Australian Journal of Zoology* 41: 399-414.
- Andersen AN. 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography* 22: 15-29.
- Andersen AN. 2000. *The Ants of Northern Australia. A Guide to the Monsoonal Fauna*. CSIRO: Collingwood.
- Andersen AN. 2002. Common names for Australian ants (Hymenoptera: Formicidae). *Australian Journal of Entomology* 41: 285-293.
- Andersen AN. 2019. Responses of ant communities to disturbance: five principles for understanding the disturbance dynamics of a globally dominant faunal group. *Journal of Animal Ecology* 88: 350-362.
- Andersen AN, Del Toro I, Parr CL. 2015. Savanna ant species richness is maintained along a bioclimatic gradient of decreasing rainfall and increasing latitude in northern Australia. *Journal of Biogeography* 42: 2313-2322.
- Andersen AN, Hoffmann BD. 2011. Conservation value of low fire frequency in tropical savannas: Ants in monsoonal northern Australia. *Austral Ecology* 36: 497-503.
- Andersen AN, Hoffmann BD, Oberprieler S. 2018. Diversity and biogeography of a species-rich ant fauna of the Australian seasonal tropics. *Insect Science* 25: 519-526.
- Andersen AN, Lanoue J, Radford I. 2010. The ant fauna of the remote Mitchell Falls area of tropical north-western Australia: biogeography, environmental

- relationships and conservation significance. *Journal of Insect Conservation* 14: 647-661.
- Andersen AN, Ribbons RR, Pettit M, Parr CL. 2014. Burning for biodiversity: highly resilient ant communities respond only to strongly contrasting fire regimes in Australia's seasonal tropics. *Journal of Applied Ecology* 51: 1406-1413.
- Anderson MJ, Gorley RN, Clarke KR. 2008. *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. PRIMER-E: Plymouth, UK.
- Arcoverde GB, Andersen AN, Setterfield SA. 2017. Is livestock grazing compatible with biodiversity conservation? Impacts on savanna ant communities in the Australian seasonal tropics. *Biodiversity and Conservation* 26: 883-897.
- Campos RI, Vasconcelos HL, Andersen AN, Frizzo TLM, Spena KC. 2011. Multi-scale ant diversity in savanna woodlands: an intercontinental comparison. *Austral Ecology* 36: 983-999.
- Clarke KR, Gorley RN. 2006. *PRIMER v6: User manual/Tutorial*. PRIMER-E: Plymouth, UK.
- Clarke KR, Warwick RM. 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. 2nd Edition*. PRIMER-E: Plymouth, UK.
- Cross AT, Myers C, Mitchell CNA, Cross S, Jackson C, Waina R, Mucina L, Dixon KW, Andersen AN. 2016. Ant biodiversity and its environmental predictors in the North Kimberley region of Australia's seasonal tropics. *Biodiversity and Conservation* 25: 1727-1759.
- Dalle Laste KC, Durigan G, Andersen AN. 2019. Biodiversity responses to land-use and restoration in a global biodiversity hotspot: Ant communities in Brazilian Cerrado. *Austral Ecology* 44: 313-326.
- Department of Environment and Heritage Protection (DEHP). (2016). *Qld REDD V10.0 December 2016*. Queensland Government: Brisbane.
- Gross CL, Whalen MA, Andrew MH. 1991. Seed selection and removal by ants in a tropical savanna woodland in northern Australia. *Journal of Tropical Ecology* 7: 99-112.
- Hoffmann BD. 2010. Using ants for rangeland monitoring: Global patterns in the responses of ant communities to grazing. *Ecological Indicators* 10: 105-111.
- Hoffmann BD, Andersen AN. 2003. Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology* 28: 444-464.
- Hoffmann BD, Griffiths AD, Andersen AN. 2000. Responses of ant communities to dry sulfur deposition from mining emissions in semi-arid tropical Australia, with implications for the use of functional groups. *Austral Ecology* 25: 653-663.
- Neldner VJ, Wilson BA, Dillewaard HA, Ryan TS, Butler DW. 2017. *Methodology for Survey and Mapping of Regional Ecosystems and Vegetation Communities in Queensland. Version 4.0. Updated May 2017*. Queensland Herbarium: Brisbane.
- Setterfield SA, Andersen AN. 2018. Seed supply limits seedling recruitment of *Eucalyptus miniata*: interactions between seed predation by ants and fire in the Australian seasonal tropics. *Oecologia* 186: 965-972.
- Silva EF, Cora JE, Harada AY, Sampaio IBM. 2017. Association of the occurrence of ant species (Hymenoptera: Formicidae) with soil attributes, vegetation, and climate in the Brazilian savanna Northeastern Region. *Sociobiology* 64: 442-450.
- State of Queensland (SoQ). 2018. *Queensland Globe*. <https://qldglobe.information.qld.gov.au/>; accessed on various occasions.
- van Ingen LT, Campos RI, Andersen AN. 2008. Ant community structure along an extended rain forest-savanna gradient in tropical Australia. *Journal of Tropical Ecology* 24: 445-455.
- Vasconcelos HL, Maravalhas JB, Cornelissen T. 2017. Effects of fire disturbance on ant abundance and diversity: a global meta-analysis. *Biodiversity and Conservation* 26: 177-188.
- Watkinson AR, Lonsdale WM, Andrew MH. 1989. Modelling the population dynamics of an annual plant *Sorghum intrans* in the Wet-dry tropics. *Journal of Ecology* 77: 162-181.
- Wilson PR, Taylor PM. 2012. *Land Zones of Queensland*. Queensland Herbarium, Queensland Department of Science, Information Technology, Innovation and the Arts: Brisbane.