Ant diversity in eucalypt woodland at Koah, the ecotone between Wet Tropics rainforests and the savannah woodlands of the Einasleigh Uplands bioregion

Scott C. Morrison[A] and *Donald C. Franklin*[B]

[A]33 Mile Creek, Koah Qld 4881, Australia. Email: scottsajidah@bigpond.com

[B]Research Institute for the Environment & Livelihoods, Charles Darwin University, Darwin NT 0909, Australia & Ecological Communications, 24 Broadway, Herberton Qld 4887, Australia

Abstract

Ants were surveyed on a 12.8 ha bush property at 33 Mile Creek, Koah, in Far North Queensland, that comprised eucalypt woodland and a small disturbed area. Pitfall trapping was conducted at eight sites in 2019 and the same sites again in 2020. Ants were also surveyed incidentally by hand collection throughout the property from 2018 to 2021. We recorded 102 species from 30 genera, of which 53 species were trapped in pitfalls. A further 49 species were recorded only incidentally, greatly enhancing the overall survey and accounting for total richness which was similar to that of other studies in the region notwithstanding their greater range of environmental variation. Ant species composition showed little correspondence to the limited variation in vegetation structure and composition, but functional guild composition showed more interpretable patterns. This included the prevalence of Dominant Dolichoderinae and Hot-Climate Specialists at an open site and a low frequency of Generalised Myrmicinae in the face of Dominant Dolichoderinae at that site. Opportunists were particularly prevalent at the site whose dry sclerophyll understorey suggests moisture stress. There was also evidence of an inverse relationship between the frequency of Opportunists and Generalised Myrmicinae. The ant fauna comprises predominately Australian endemics of Torresian (tropical) biogeographical origin. At least 41 species are only known from Queensland. Five species are not native to Australia, all of which are widespread tramp ants.

Handling editor: Peter Valentine

Citation: Morrison SC, Franklin DC. 2022. Ant diversity in eucalypt woodland at Koah, the ecotone between Wet Tropics rainforests and the savannah woodlands of the Einasleigh Uplands bioregion. *North Queensland Naturalist* 52: 34-46.

Introduction

Ants are highly diverse in numerous Australian environments including the arid zone, savannas and wet tropics rainforests (Andersen 2016; Nowrouzi *et al.* 2016; Andersen *et al.* 2018, 2020). They are a globally dominant faunal group (Andersen & Vasconcelos 2022), and can account for large percentages of total animal biomass (Hölldobler & Wilson 1990).

Based on responses of ant fauna to environmental stress and disturbance, seven functional groups are recognised (Andersen 1995). The north Australian savanna fauna features particular prevalence of 'Dominant Dolichoderinae' (mainly *Iridomyrmex* [tyrant ants, meat ants] species), 'Generalised Myrmicinae' (especially *Monomorium* [mono ants] and *Pheidole* [big-headed ants] species) and 'Hot-

Climate Specialists' (particularly *Melophorus* [furnace ants] and *Meranoplus* [shield ants] species) (Andersen 2000; Andersen *et al.* 2015). 'Dominant Dolichoderinae' and 'Hot-Climate Specialists' prefer more open environments (Hoffmann & Andersen 2003). 'Generalised Myrmicinae' and 'Opportunists' are habitat generalists that tend to be excluded by aggressive 'Dominant Dolichoderinae' (Andersen & Patel 1994; Hoffmann & Andersen 2003). The relative abundance of 'Generalised Myrmicinae' and 'Opportunists' tend also to be negatively related to each other because most Opportunists are tolerant of stress and disturbance but most Generalised Myrmicinae are not (Hoffmann & Andersen 2003). 'Opportunists' feature at environmentally stressed sites with low ant diversity (Hoffmann & Andersen 2003).

In this study, we evaluate the ant assemblage of a lowland (370 m ASL) eucalypt woodland site with a few rainforest elements and a creekline (33 Mile Creek) near the boundary between the Wet Tropics and Einasleigh Uplands bioregions. This builds on previous ant studies from these bioregions by King *et al.* (1998), Woinarski *et al.* (2002), van Ingen *et al.* (2008), Nowrouzi *et al.* (2016), Lawes *et al.* (2017) and Franklin & Morrison (2019). In these bioregions, the ant faunas of savannas and rainforest/wet sclerophyll forest are quite distinct (van Ingen *et al.* 2008), with savannas supporting greater species richness.

Methods

Study area

33 Mile Creek, Koah (16°50'S, 145°30'E; 370 m ASL) is a subcatchment of the Barron River near the confluence of the Clohesy and Barron Rivers in the rainshadow of the coastal ranges of the Wet Tropics bioregion. Though in the Wet Tropics bioregion, the study site is *c.* 1 km from the eastern boundary of the Einasleigh Uplands bioregion and features eucalypt vegetation rather than rain-forest. This is reflected in the mean annual rainfall of 1128 mm reported for Koah, contrasting drastically with Kuranda in the Wet Tropics bioregion 14 km to the east (2025 mm; elevation 340 m ASL), and less so with Biboohra in the Einasleigh Uplands 13.5 km to the south-west (920 mm; elevation 375 m) (Bureau of Meteorology 2022). The area is thus more akin to the Einasleigh Uplands than the nearby rainforested mountains of the Wet Tropics.

The study site is a private allotment of 12.8 ha, most of which supports remnant vegetation which is contiguous, via other private allotments also mostly forested, with Dinden Forest Reserve to the south, Bilwon State Forest to the west and Kuranda State Forest to the north. About 0.5 ha of the study site was cleared for a homestead in *c.* 1998 (Business Queensland 1998). Evidence of selective timber harvesting, including of *Eucalyptus* species and *Callitris intratropica* (Northern Cypress-pine), exists across the property. 33 Mile Creek runs diagonally across a corner of the block for 280 m.

Soils on the allotment consist of poorly-drained, infertile clays with a gritty and at times sandy surface and rarely with lateritic gravels present. These are "poorly consolidated sediments" of late Tertiary-Quaternary origins (Detailed surface geology coverage, Qld Govt 2021). Outcropping rock is uncommon and limited to the vicinity of 33 Mile Creek. The creek has incised the sediments to a depth of up to 7 m such that that the entire allotments slopes, often steeply, down to the creek.

Remnant vegetation is mostly 10-18 m tall woodland to open forest (e.g. Fig. 1). *Corymbia clarksoniana* (Clarkson's Bloodwood), *Eucalyptus portuensis* (White Mahogany), *Melaleuca viridiflora* (Broad-leaved Paperbark), *Callitris intratropica* and *Allocasuarina littoralis* (Black She-oak) are almost universally present, with one or more species dominant but in varying proportions. The ground layer is predominantly the perennial grass *Eriachne triseta* (Wanderrie Grass). The rainforest shrub or vine *Alyxia spicata* (Chainfruit) and tree *Alstonia muelleriana* (Milkwood) are widely dispersed on the allotment but non-dominant; these are noted as common species that support the transition process from open to closed woodlands and forest habitats through an absence and reduction in fire frequency (Stanton *et al* 2014a,b). Although the vegetation is transitional between woodland and dry open forest, it is nearer to woodland and for simplicity will hereafter be referred to as woodland. Fire scars are present on tree trunks of various diameter across the property, but aside from a strategic low intensity, mid dry season burn of 1.7 ha in 2020, the area has remained unburnt for at least 30 years (Sam Musumeci, Fire warden, Queensland Rural Fire Service and long-term resident, personal communication 2020; Nafi3 2022).

Figure 1. Eucalypt woodland on the study allotment, 33 Mile Creek, Koah, north Queensland.
Photo: Scott Morrison.

The allotment is mapped as supporting Regional Ecosystems (REs) 7.11.14a, 7.11.35a and 7.3.14a (Queensland Government 2021), all of which have a biodiversity status of "Of Concern". However, we note that the land systems underlying these (11 = metamorphic, 3 = alluvial; Wilson & Taylor 2012) are incorrect descriptions of the allotment, and that the floristics of the REs provide, at best, only a moderately good match.

Field methods

Eight sites were selected to represent the diversity of vegetation and disturbance present on the property, including one on the edge of and mostly within the cleared area (Site 8), and one on the bank of 33 Mile Creek (Site 2). Ants were sampled in each of the eight sites using 15 pitfall traps per site on 22-24 November 2019 and again on 21-23 Nov. 2020. Pitfall traps were plastic containers 45 mm in diameter and 55 mm deep that were half-filled with 50% ethylene glycol solution and buried with the rim flush to the ground. The traps were spaced 10 m apart in a 5 x 3 grid, set for 48 hours. Ants were also hand-collected opportunistically across the property from 2018 to 2021.

In 2019, conditions during the survey were sunny and dry with daily minimums of *c.* 16°C and maximums of *c.* 32°C, with 0.25 mm of rain. In 2020, daily minimums reached *c.* 21°C and maximums *c.* 30°C, and conditions ranged from overcast with light squalls to sunny, with 14.5 mm rain falling over the trapping period. On neither occasion did traps overfill due to rainfall. Rainfall in the 12 months prior to trapping also varied marked between years – 1465 mm prior to the 2019 survey and 900 mm prior to the 2020 survey.

The following environmental variables were assessed on 31 August 2019 in a 50 x 30 m plot surrounding the pitfall array of each site:

- cover class and height of four vegetation strata: trees, small trees (generally less than 60% of canopy height), shrubs and herbs (graminoids & forbs);
- cover class of each woody plant species present; and
- cover class of rocks.

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.

Asset protection burns conducted in July and August 2020, i.e. between pitfall surveys, resulted in sites 1 and 5 being burnt. These sites were assessed on 15 October 2020 as having low to minimum crown scorch with patchy, low intensity burning of the ground layer.

Data analysis

Ants were sorted to species by SCM and a pinned voucher collection was verified and is held by AN Andersen (Charles Darwin University). Species that could not be named were attributed to species groups or assigned codes which are the same as have been applied in other studies in Queensland and across northern Australia by AN Andersen and associates. Species were then classified into functional groups in relation to environmental stress and disturbance following Andersen (1995) and Hoffmann (2000). Where common names for ants are available, they firstly follow Andersen (2002), then Deyrup *et al.* (2000).

The primary ant metric employed in this study is frequency of occurrence (FoO), which is the number of traps in which the species was detected for each site in each sampling period. From this we derived *summed frequencies of occurrence* (summed FoO), which are the sum of species FoOs for each of sub-families and functional groups.

Ant species were classified as:

- native or not; and
- endemic to Australia, or also occurring in islands to our north and/or in south-east Asia, or pantropical, or widespread.

For a sub-set of species for which sufficient information was available, we further classified them as:

- having a Torresian (tropical), Eyrean (arid) or widespread distribution within Australia. Noting none had a Bassian (temperate) distribution; and
- within northern Australia, being confined to Wet Tropics rainforest, otherwise restricted to Queensland, or widespread across northern Australia.

The above distributional information was extracted from King *et al.* (1998), van Ingen *et al.* (2008) and Andersen *et al.* (2018), and also interpreted from antmaps.org (2022 – see Janicki *et al.* (2016) and Guénard *et al.* (2017)), AntWeb (2022) and Antwiki (2022), occasionally from other sources. Biogeographical affinities are based on Spencer (1896) and are as applied by various authors, for example Andersen (2000), Heterick *et al*. (2010) and Ebach and Murphy (2020).

The relative similarity of sites based on their woody plant cover, and site-years based on the ant structure (each of species, sub-family, functional group), were compared in multi-dimensional ordination space. Ordinations are Non-metric multidimensional scaling with the Bray-Curtis similarity measure, the data having been square-root transformed. The ordination was performed in Primer v6 (Clarke & Gorley 2006) and a paired t-test and correlation analysis in Statistica 13.2 (Dell Inc. 1984-2016).

Results

The ant fauna

A total of 102 ant species were identified, of which 53 were collected in pit-fall traps and 49 more were collected opportunistically. The 102 species represent 6 sub-families and 8 functional groups (Table 1). The sub-families Myrmicinae and Formicinae were the most speciose sub-families pitfall trapped. Myrmicinae was numerically dominant in the abundance metric (summed FoO). Subordinate Camponotini, along with Opportunists and Generalised Myrmicinae, were the most speciose functional groups.

Five non-native ant species were recorded, of which four were Opportunists (Table 2). Only two of these were trapped, these two being widespread in the woodland (Table 2). Three species were recorded only opportunistically and found only at the homestead.

Site vegetation

Ordination of sites based on woody plant cover confirms the aberrant nature of the disturbed site 8 (Fig. 2A), this being driven by the presence of six species of fruit tree and reduced cover and diversity of woodland species. The remaining seven woodland sites clustered strongly in that ordination, all supporting *Acacia flavescens* (Primrose Wattle), *A. leptocarpa* (North Coast Wattle) *Allocasuarina littoralis*, *Alyxia spicata* and *Corymbia clarksoniana* which were absent from or at reduced cover at site 8. *Callitris intratopica*, *Eucalyptus portuensis* (syn. *E. mediocris*, *E. acmenoides*), *Grevillea mcgillivrayi* (Fine-leaved Beefwood; previously *G. coriacea*) and *Melaleuca viridiflora* were also present at most or all open forest sites.

An ordination of the seven woodland sites (Fig. 2B) revealed more subtle variation among them with four groupings or individual sites. Sites 3 and 4 uniquely shared the presence of the dry country shrubs *Acacia calyculata* (a wattle), *Grevillea glauca* (Bushman's Clothes Pegs), *Jacksonia thesioides* (Jacksonia) and *Xanthorrhoea johnsonii* (Northern Forest Grass-tree), along with particularly high cover of *E. portuensis* and low cover of *Alyxia spicata*, possibly driven by shallower, more gravelly soils. Sites 5, 6 and 7 differed from 3 and 4 in woody plant cover primarily in lacking dry country shrubs. Sites 1 and 2 were moister sites, Site 1 on a slope but with much seepage and particularly poor drainage and a notably high cover of *M. viridiflora*, and Site 2 near 33 Mile Creek with higher cover than any other plot of *Parinara nonda* (Nonda Plum) and *Alstonia muelleriana*, the two sites sharing the unique presence of *Lophostemon suaveolens* (Sweet Honey-myrtle) and *Breynia stipitata* (Dwarf's Apple; syn. *B. cernua*) though the latter at very low cover. We thus treat the eight sites as representing five habitat groups comprising the disturbed site plus four woodland groups.

Table 1. Abundance measures for ant sub-families, most speciose genera and functional groups recorded at 33 Mile Creek, Koah, far north Queensland.
Total no. (%) of species combines trapping and opportunistic observations.
A full list of species with their functional groups and FoO at each site, is provided in Appendix 1.

Taxon/Functional Group	Total no. (%) of species	Trapped no. (%) of species	Trapped summed FoO (%)	No. (%) of trap sites (n = 8)
Sub-family				
Dorylinae	2 (2.0)	0	0	0
Ponerinae	6 (5.9)	2 (3.8)	5 (0.9)	2 (25)
Ectatomminae	4 (3.9)	3 (5.7)	37 (6.4)	3 (37.5)
Myrmicinae	36 (35.3)	24 (45.3)	257 (44.5)	8 (100)
Dolichoderinae	17 (16.7)	12 (22.6)	135 (23.4)	8 (100)
Formicinae	37 (36.3)	12 (22.6)	144 (24.9)	8 (100)
Most speciose genera (Total >6 species)				
Polyrhachis (Formicinae, Subordinate Camponotini)	16 (15.7)	1 (1.9)	1 (0.2)	1 (2.5)
Iridomyrmex (Dolichoderinae, Dominant Dolichoderinae)	9 (8.8)	8 (15.1)	128 (22.1)	8 (100)
Monomorium (Myrmicinae, Generalised Myrmicinae)	8 (7.8)	7 (13.2)	67 (11.6)	8 (100)
Crematogaster (Myrmicinae, Generalised Myrmicinae)	7 (6.9)	3 (5.7)	9 (1.6)	4 (50)
Tetramorium (Myrmicinae, Opportunists)	7 (6.9)	4 (7.5)	35 (6.1)	7 (87.5)
Functional group				
Dominant Dolichoderinae	10 (9.8)	8 (15.1)	128 (22.1)	8 (100)
Subordinate Camponotini	25 (24.5)	3 (5.7)	9 (1.6)	4 (50)
Hot-Climate Specialists	7 (6.9)	6 (11.3)	59 (10.2)	7 (87.5)
Tropical-Climate Specialists	5 (4.9)	3 (5.7)	32 (5.5)	6 (75)
Cryptic species	4 (3.9)	1 (1.9)	43 (7.4)	6 (75)
Opportunists	25 (24.5)	17 (32.1)	155 (26.8)	8 (100)
Generalised Myrmicinae	20 (19.6)	14 (26.4)	148 (25.6)	8 (100)
Specialist Predator	6 (5.9)	1 (1.9)	4 (0.7)	1 (12.5)
Total	**102**	**53**	**578**	**8**

Table 2. Non-native ant species recorded at 33 Mile Creek, Koah.

Species	Common name	Sub-family	Functional group	Occurrence
Monomorium floricola	Bicoloured Trailing Ant	Myrmicinae	Generalised Myrmicinae	opportunist observation only
Tetramorium bicarinatum	Guinea Groove-headed Ant	Myrmicinae	Opportunist	opportunist observation only
Tetramorium simillimum	Similar Groove-headed Ant	Myrmicinae	Opportunist	common; trapped most sites
Tapinoma melanocephalum	Ghost Ant	Dolichoderinae	Opportunist	opportunist observation only
Paratrechina longicornis	Black Crazy Ant	Formicinae	Opportunist	common; trapped many sites

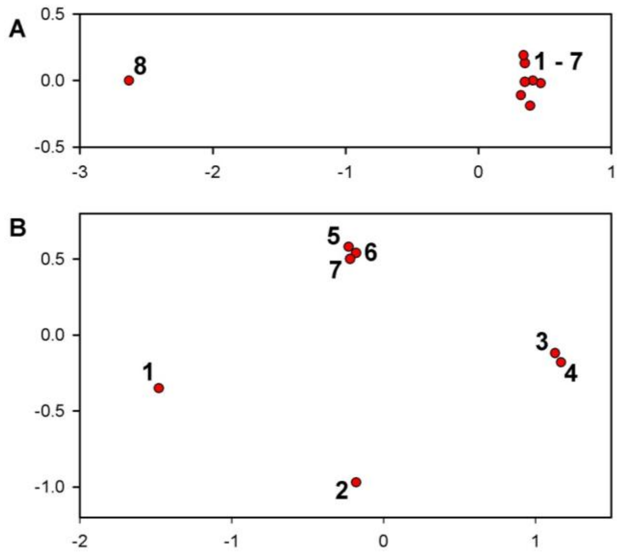

Figure 2. Two-dimensional NMDS ordinations of sites on cover of woody plant species: A. all eight sites; and B. the seven woodland sites.
Both ordinations are very low stress – 0.01.

All sites had greater than 50% grass cover, and all had some cover of other graminoids all at less than 25% cover. Other herbs were absent or present at less than 5% cover except at the disturbed site where cover was 10–25%, herb cover doubtless being much affected by the vegetation survey being conducted in the dry season.

Ant assemblages at sites

More ants were trapped in 2019 (48 spp., 2274 individuals) than in 2020 (35 spp., 928 individuals), including more Generalised Mymicinae (+4 spp.), Opportunists (+4 spp.), Hot Climate Specialists (+3 spp.) and Tropical Climate Specialists (+2 spp). However, five species were only trapped in 2020. Mean species per site was 16.4 in 2019 but only 8.4 in 2020, the decrease occurring at all sites and the difference being very highly significant (paired-sample t-test, $t = 8.83$, d.f. $= 7$, $P < 0.0001$). Over the two years of trapping, 19 species out of 53 (36%) were trapped at one site only, with 15 of those (28%) in a single trap only.

Ant species assemblage compositions were more tightly clustered in ordination space in 2019 than 2020, with the direction of change over time dispersed outwards in multiple directions in the ordination (Fig. 3A). This likely reflects greater noise associated with small samples in 2020, suggesting that the 2019 data offers greater potential for interpretation. Nevertheless, even for 2019, there was no clear correspondence of ant species composition with the patterns of woody vegetation evident in Fig. 2, even the highly disturbed site 8 being not differentiable from woodland sites. Nor was there any obvious effect of the burns on the 2020 data other than that, perhaps counterintuitively, the distance in ordination space between site pairs across years was least in the two sites burnt between surveys, indicating least change in species composition.

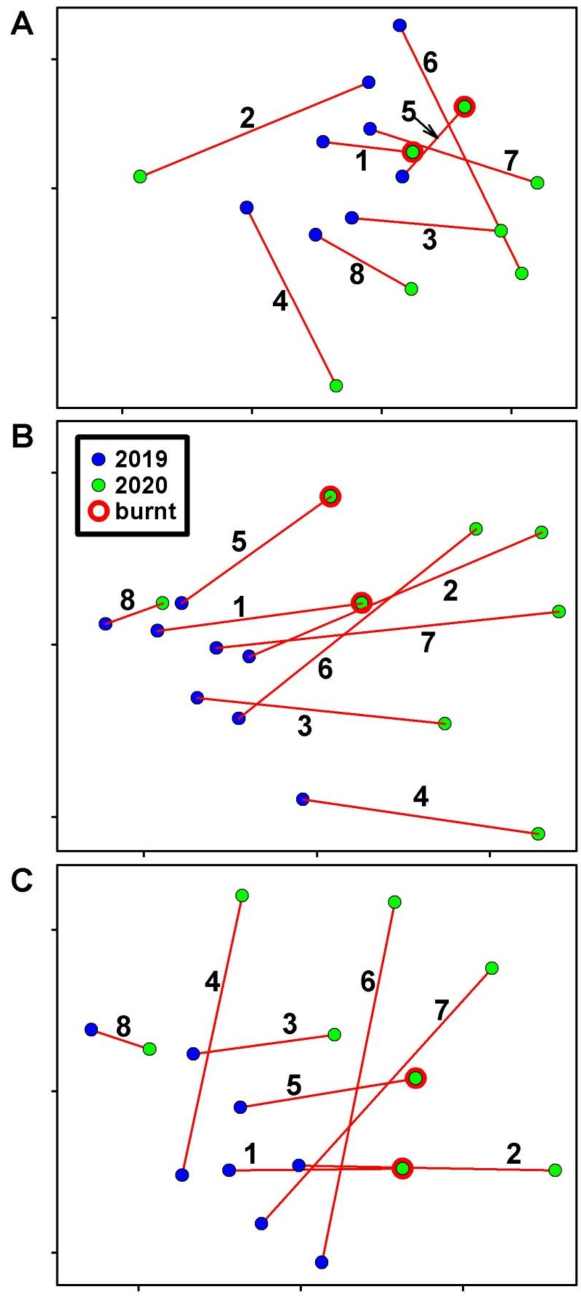

Figure 3. Two-dimensional NMDS ordinations of sites (each year separately) on: A. ant species frequency of occurrence; B. sub-family summed frequency of occurrence; and C. functional group summed frequency of occurrence.

However, sub-familial and functional group composition (Figs. 3B & 3C respectively) showed more readily interpretable patterning. In both, the highly disturbed Site 8 showed markedly less year-to-year variation than woodland sites and some tendency to be an outlier. As with species composition, sub-familial and functional group composition was much more consistent across sites in 2019 than 2020. The direction of change in ordination space over time was most consistent in sub-familial composition, generally from left to right in ordination space (Fig. 3B).

We offer the following interpretation of these ordination patterns based on data presented in Tables 3 and 4. The relatively open Site 8 stands out for having a very high frequency of Dolichoderinae and higher frequency of Ponerinae ants, and among functional groups it stands out for a higher frequency of Dominant Dolichoderinae, Hot-Climate Specialists, Opportunists and Specialist Predators, and a low frequency of Generalised Myrmicinae. The woodland sites 5, 6 & 7 which lacked dry country shrubs aggregate based particularly on a low frequency of Opportunists. The creekside Site 2 lacked any outstanding sub-family or functional group characters. The poorly-drained slope Site 1 had a high prevalence of Dominant Dolichoderinae compared to other woodland sites but not as high as the disturbed Site 8, along with a generally high prevalence of Generalised Myrmicinae. Across the eight sites, there was a negative relationship between Generalised Myrmicinae and Opportunists ($r^2 = 0.41$) though the evidence is weak ($P = 0.088$).

Table 3. Summed frequency of occurrence of sub-families for eight sites at 33 Mile Creek, Koah, 2019.
The five habitat groups are shown in alternating grey and white highlights (from Fig. 2); their ant features relative to other sites (i.e. horizontally across the table) are highlighted in the table body, with pink = high values.

Sub-family	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
Ponerinae	0	0	0	0	0	1	0	3
Ectatomminae	0	0	4	13	0	0	0	0
Myrmicinae	28	21	27	14	28	17	29	31
Dolichoderinae	23	3	9	1	19	1	4	32
Formicinae	17	12	19	15	9	16	12	20

Table 4. Summed frequency of occurrence of functional groups for eight sites at 33 Mile Creek, Koah, 2019.
The five habitat groups are shown in alternating grey and white highlights (from Fig. 2); their ant features relative to other sites (i.e. horizontally across the table) are highlighted in the table body: yellow = low values; pink = high values.

Functional group	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
Dominant Dolichoderinae	23	1	9	1	16	0	4	31
Subordinate Camponotini	1	1	0	0	2	3	0	0
Hot-Climate Specialist	4	1	10	5	0	4	6	16
Tropical Climate Specialist	0	1	0	0	0	1	0	0
Cryptic species	0	0	10	0	8	0	0	10
Opportunist	13	15	21	23	11	5	5	22
Generalised Myrmicinae	25	16	5	14	16	14	23	4
Specialist Predator	0	0	0	0	0	0	0	3

Biogeography

Most ant species were Australian endemics (83.3%), with 7.8% occurring also only as far as south-east Asia, 4.9% have a pantropical distribution and 3.9% are even more widespread (Appendix 1). Within Australia, of 90 species that could be classified, most are Torresian and none were Bassian (Table 5). Within northern Australia, of the 72 species that could be classified, one (*Polyrhachis delecta*, detected only opportunistically; see Kohout 2006) is endemic to Wet Tropics rainforest, 40 are otherwise endemic to Queensland and 31 also occur in the north of the Northern Territory and Kimberley region of Western Australia.

Discussion

Across Australia, high species richness of ants can be seen at both local (Andersen 1983) and continental levels, particularly so in the monsoonal tropics (Andersen *et al.* 2020, 2022) such as in the Einasleigh Uplands bioregion. Species richness of 102 species from 30 genera in this study, notwithstanding limited variation in habitat, was similar to that of other surveys in the bioregion which involved a greater range of habitats: van Ingen *et al*. (2008) – 95 species, 35 genera; Franklin & Morrison (2019) – 133 species, 24 genera. However, in this study, 49 species were only detected opportunistically, an additional survey method and considerable enhancement not reported in either of the other studies. In our study, trapping was somewhat limited (pitfalls at eight sites over two sessions) due in good part to the small area being surveyed (12.8 ha; much smaller than either of the above) with limited range of habitats, but opportunistic surveys occurred over four years. Species that were only hand collected are often those that stand out, for example *Polyrachis* (Spiny Ants) and Specialized Predators. In contrast, pitfall trapping can deliver a picture of ant assemblages that is repeatable over time and comparable across space (Steiner *et al.* 2005).

The high incidence of species trapped at only one site or even only in one trap strongly suggests that further trapping in the study area would yield more trapped species. However, potential additions might have already been detected opportunistically. Winkler traps might also detect additional subterranean and cryptic species. A similar incidence of “rare” species was recorded in traps by Franklin & Morrison (2019), who demonstrated using a species accumulation curve that further trapping was likely to yield more than the 133 species recorded.

The greater abundance and species richness in the 2019 than 2020 trapping session was likely due to more sunshine and less rain during the trapping period, and perhaps also to considerably greater antecedent rainfall in the former, creating more favourable environmental conditions.

That ant species composition showed little correspondence to vegetation structure or composition (even in 2019 when ants were trapped in greater numbers and variety) may partly be the result of small sample size (eight sites). Limited variation in soil and habitat within the study area may also have limited ability to discern patterns; Franklin & Morrison (2019) documented that variation in ant species composition was related to vegetation along a much more marked soil gradient.

In this study, however, when data were pooled up to sub-families and especially to functional guilds, meaningful patterns emerged. As expected from the prior findings of Hoffmann and Andersen

Table 5. Australian biogeographical affinities (% of species) of ants in three north Queensland studies. For this study, 90 of 102 species were classified.

Biogeographic group	King *et al.* (1998)*	van Ingen *et al.* (2008)**	Koah, this study
Torresian	60	53.7	68.9
Eyrean	0	8.4	12.2
Widespread	28	23.2	18.9
Bassian	12	14.7	0
Total	**100**	**100**	**100**

* in rainforest and cleared rainforest on the Atherton Tableland

** along a transect from rainforest to savanna near Mount Molloy

(2003), the heat-loving Dominant Dolichoderinae and Hot-Climate Specialists were most abundant at the open Site 8. Generalised Myrmicinae were least abundant at Site 8, as predicted based on competitive exclusion by Dominant Dolichoderinae, but contrary to expectation, Opportunists were abundant there notwithstanding the abundance of Dominant Dolichoderinae. The notable abundance of Opportunists at sites 3 and 4 is consistent with the suggestion that their dry sclerophyll understorey indicates relative moisture stress. The negative relationship between Generalised Myrmicinae and Opportunists found by Hoffmann & Andersen (2003) also appears to be present among sites in the study area.

The explanation for other evident patterns is less clear. The abundance of Dominant Dolichoderinae at Site 1 might be because that site had low cover of small trees and shrubs (unpublished data) increasing ground insolation and therefore favouring the abundance of dominant *Iridomyrmex* species which are most common in open habitats (Andersen 2000). Notably, despite a prevalence of Dominant Dolichoderinae, Site 1 also has a high FoO of Generalised Myrmicinae, which may be explained by niche partitioning at the species level due to: (1) the nocturnal nature of *Monomorium leave* group (Andersen *et al.* 2013); (2) the close morphological affinity of *M. sordidum* group to the Hot Climate Specialist *M. rostheni* group (Sparks 2015); and (3) the arboreal nature of *Crematogaster* species (Andersen 2000). These genera comprised 48% of Generalised Myrmicinae at Site 1.

The majority of ants at Koah were Australian endemics associated with the tropical savanna biome. The absence of Bassian (temperate-zone) species at Koah but their presence in two other north Queensland studies (Table 5) doubtless reflects that those studies both included sites at higher elevation rainforest. The five non-native species recorded are all tramp ants – species that are easily dispersed by human activity (Passera 1994). All are widespread in tropical and sometimes also temperate latitudes worldwide (Andersen 2000; AntWeb 2022; Antwiki 2022), and have been recorded at other sites in the Wet Tropics and Einasleigh Uplands (Woinarski *et al.* 2002; Andersen *et al*. 2004; Nowrouzi *et al*. 2016; Franklin & Morrison 2019).

Acknowledgements

We are grateful to the following for both field assistance and plant identification: Sajidah Abdullah, Matt Bradford, Kylie Freebody, Simon Gleed, Kell Morrison, Thor Morrison, Dave Rentz, Fanie Venter and Gary Wilson. Also to Professor Alan N. Andersen, Charles Darwin University, who identified all hand collected species and confirmed identification of pinned specimens. We thank two anonymous reviewers whose comments have led to substantial improvements to this manuscript.

References

Andersen AN. 1983. Species diversity and temporal distribution of ants in the semi-arid mallee region of north-western Victoria. *Austral Ecology* 8: 127-137.

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. 2016. Ant megadiversity and its origins in arid Australia. *Austral Entomology* 55: 132-137.

Andersen AN, Patel AD. 1994. Meat ants as dominant members of Australian ant communities: an experimental test of their influence on the foraging success and forager abundance of other species. *Oecologia* 98: 15-24.

Andersen AN, Woinarski JCZ, Hoffmann BD. 2004. Biogeography of the ant fauna of the Tiwi Islands, in northern Australia's monsoonal tropics. *Australian Journal of Zoology* 52: 97-110.

Andersen AN, Arnan X, Sparks K. 2013. Limited niche differentiation within remarkable co-occurrences of congeneric species: *Monomorium* ants in the Australian seasonal tropics. *Austral Ecology* 38: 557-567.

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, Oberprieler S. 2018. Diversity and biogeography of a species-rich ant fauna of the Australian seasonal tropics. *Insect Science* 25: 519-526.

Andersen AN, Hoffmann BD, Oberprieler S. 2020. Megadiversity in the ant genus *Melophorus*: the *M. rufoniger* Heterick, Castalanelli and Shattuck species group in the Top End of Australia's Northern Territory. *Diversity* 12: Art. no. 386.

Andersen AN, Brassard F, Hoffmann BD. 2022. Unrecognized ant megadiversity in monsoonal Australia: Diversity and its distribution in the hyperdiverse *Monomorium nigrius* Forel group. *Diversity* 14: Art. no. 46.

Andersen AN, Vasconcelos HN. 2022. Historical biogeography shapes functional ecology: Inter-continental contrasts in responses of savanna ant communities to stress and disturbance. *Journal of Biogeography* 49: 590-599.

Antmaps.org. 2022. *https://antmaps.org/*, viewed 22 May 2022.

AntWeb. 2022. Version 8.73. California Academy of Science. *https://www.antweb.org*, viewed multiple times, Feb. 2022.

Antwiki. 2022. *https://www.antwiki.org*, viewed multiple times, Feb. 2022.

Bureau of Meteorology. 2022. Australian Government. *www.bom.gov.au*, viewed 12 March 2022.

Business Queensland. 1998. Land title survey plan SP110317.

Clarke KR, Gorley RN. 2006. *PRIMER v6: User Manual/ Tutorial*. PRIMER-E: Plymouth, UK.

Dell Inc. 1984-2016. *Statistica 13.2*. Dell Inc.: Round Rock, Texas.

Deyrup M, Davis L, Cover S. 2000. Exotic ants in Florida. *Transactions of the American Entomological Society* 126: 293-326.

Ebach MC, Murphy DJ. 2020. Carving up Australia's arid zone: a review of the bioregionalisation of the Eremaean and Eyrean biogeographic regions. *Australian Journal of Botany* 68: 229-244.

Franklin DC, Morrison SC. 2019. The ants of Talaroo Station: diversity, composition and habitat associations of a tropical savanna insect assemblage. *North Queensland Naturalist* 49: 65-77.

Guénard B, Weiser M, Gomez K, Narula N, Economo EP. 2017. The Global Ant Biodiversity Informatics (GABI) database: a synthesis of ant species geographic distributions. *Myrmecological News* 24: 83-89.

Heterick BE, Durrant B, Gunawardene NR. 2010. The ant fauna of the Pilbara Bioregion, Western Australia. *Records of the Western Australian Museum*, Supplement 78: 157-167.

Hoffmann BD. 2000. *Responses of Ant Communities to Land Use Impacts in Australia*. PhD thesis, Northern Territory University: Darwin.

Hoffmann BD, Andersen AN. 2003. Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology* 28: 444-464.

Hölldobler B, Wilson EO. 1990. *The Ants*. Harvard University Press: Cambridge, Mass., USA.

Janicki J, Narula N, Ziegler M, Guénard B, Economo EP. 2016. Visualizing and interacting with large-volume biodiversity data using client-server web-mapping applications: The design and implementation of antmaps.org. *Ecological Informatics* 32: 185-193

King JR, Andersen AN, Cutter AD. 1998. Ants as bioindicators of habitat disturbance: validation of the functional group model for Australia's humid tropics. *Biodiversity and Conservation* 7: 1627-1638.

Kohout RJ. 2006. New species of the *Polyrhachis* (*Myrma*) *parabiotica* species group (Hymenoptera: Formicidae: Formicinae) from the Philippines. *Australian Entomologist* 3: 155-163.

Lawes MJ, Moore AM, Andersen AN, Preece ND, Franklin DC. 2017. Ants as ecological indicators of rainforest restoration in the Australian wet tropics. *Ecology and Evolution* 7: 8442-8455.

Nafi3. 2022. North Australia and Rangelands Fire Information. *https://firenorth.org.au/nafi3/*, viewed 2 February 2022.

Nowrouzi S, Andersen AN, Macfadyen S, Staunton KM, VanDerWal J, Robson SKA. 2016. Ant diversity and distribution along elevation gradients in the Australian Wet Tropics: The importance of seasonal moisture stability. *PLoS ONE* 11: e0153420.

Passera L. 1994. Characteristics of tramp species. In *Exotic Ants: Biology, Impact, and Control of Introduced Species*, ed. DF Williams, pp. 23-43. Westview Press: Boulder, Colorado.

Queensland Government 2021. Queensland Globe release 2.13. *https://qldglobe.information.qld .gov.au/*, viewed 14 April 2022.

Sparks K. 2015. Australian *Monomorium*: Systematics and species delimitation with a focus on the *M. rothsteini* complex. PhD. thesis. University of Adelaide: Adelaide.

Spencer WB. 1896. Summary of the zoological, botanical and geological results of the expedition. Report on the work of the Horn Expedition to Central Australia. Dulau: London, U.K.

Stanton P, Parsons M, Stanton D, Stott M. 2014a. Fire exclusion and the changing landscape of Queensland's Wet Tropics bioregion 2. The dynamics of transition forests and implications for management. *Australian Forestry* 77: 58-68.

Stanton P, Stanton D, Stott M, Parsons M. 2014b. Fire exclusion and the changing landscape of Queensland's Wet Tropics bioregion 1. The extent and pattern of transition. *Australian Forestry* 77: 51-57.

Steiner FM, Schlick SBC, Moder K, Bruckner A, Christian E. 2005. Congruence of data from different trapping periods of ant pitfall catches (Hymenoptera: Formicidae). *Sociobiology* 46: 105-116.

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.

Wilson PR, Taylor PM. 2012. *Land Zones of Queensland*. Queensland Herbarium, Queensland Department of Science, Information Technology, Innovation and the Arts: Brisbane.

Woinarski JCZ, Andersen AN, Churchill TB, Ash AJ. 2002. Response of ant and terrestrial spider assemblages to pastoral and military land use, and to landscape position, in a tropical savanna woodland in northern Australia. *Austral Ecology* 27: 324-333.

Appendix 1. Ant species detected by pitfall trapping and hand collection at 33 Mile Creek, Koah.
gp. = group; * indicates introduced species
Distr1 describes whether the species is endemic to Australia (end), or if not then extending no further than south-east Asia (Indo), pantropical (pan), or even more widespread (W).
Distr2 describes the species' distribution within Australia: T – Torresian; E – Eyrean; W – Widespread; na = not assigned.
Distr3 describes the species distribution within northern Australia: rf – endemic to Wet Tropics rainforest; Qld – otherwise endemic to Queensland; W = occurs further west in Northern Australia (i.e. in the Northern Territory and Kimberley); na = not assigned.

Sub-family and species	Functional group	N sites	N traps	Distr1	Distr2	Distr3
Dorylinae						
Aenictus turneri	Specialist Predator	0	0	end	W	W
Lioponera longitarsus	Specialist Predator	0	0	pan	W	W
Ponerinae						
Anochetus ?rufostenus	Specialist Predator	0	0	end	T	Qld
Anochetus sp. A (*graeffei* gp.)	Specialist Predator	0	0	end	T	Qld
Brachyponera croceicornis	Tropical Climate Specialist	1	1	Indo	T	Qld
Brachyponera lutea	Cryptic species	0	0	end	T	W
Leptogenys adlerzi	Specialist Predator	1	4	end	T	Qld
Leptogenys fallax	Specialist Predator	0	0	end	T	W
Ectatomminae						
Odontomachus nr. *turneri*	Opportunist	0	0	end	T	Qld
Rhytidoponera metallica	Opportunist	1	4	end	W	Qld
Rhytidoponera nr. *metallica*	Opportunist	2	13	end	na	Qld
Rhytidoponera ?tenuis	Opportunist	3	20	end	T	na
Myrmicinae						
Aphaenogaster barbara	Opportunist	0	0	end	T	Qld
Aphaenogaster pythia	Opportunist	3	7	Indo	T	Qld
Cardiocondyla atalanta	Opportunist	3	14	end	W	W
Cardiocondyla 'nuda'	Opportunist	1	1	pan	T	W
Cardiocondyla wroughtoni	Opportunist	2	2	pan	T	W
Crematogaster sp. A (*cornigera* gp.)	Generalised Myrmicinae	0	0	end	T	Qld
Crematogaster sp. B (*cornigera* gp.)	Generalised Myrmicinae	0	0	end	T	Qld
Crematogaster sp. A (*laeviceps* gp.)	Generalised Myrmicinae	4	7	end	T	Qld
Crematogaster sp. B (*laeviceps* gp.)	Generalised Myrmicinae	1	1	end	na	Qld
Crematogaster sp. C (*laeviceps* gp.)	Generalised Myrmicinae	0	0	end	na	Qld
Crematogaster sp. Y (group A)	Generalised Myrmicinae	1	1	end	na	na
Crematogaster sp. 10 (*australis* complex)	Generalised Myrmicinae	0	0	end	W	W
*Monomorium floricola**	Generalised Myrmicinae	0	0	pan	T	W
Monomorium sp. A (*rothsteini* gp.)	Hot-Climate Specialist	3	7	end	E	na
Monomorium sp. C1 (*carinatum* gp.)	Generalised Myrmicinae	1	1	end	T	Qld
Monomorium sp. L1 (*laeve* gp.)	Generalised Myrmicinae	7	23	end	T	Qld
Monomorium sp. L2 (*laeve* gp.)	Generalised Myrmicinae	6	14	end	T	Qld
Monomorium sp. N1 (*nigrius* gp.)	Generalised Myrmicinae	1	1	end	T	Qld

Appendix 1 continued

Sub-family and species	Functional group	N sites	N traps	Distr1	Distr2	Distr3
Monomorium sp. N2 (*nigrius* gp.)	Generalised Myrmicinae	1	1	end	T	Qld
Monomorium sp. S1 (*sordidum* gp.)	Generalised Myrmicinae	5	20	end	E	Qld
Pheidole impressiceps	Generalised Myrmicinae	3	6	Indo	T	W
Pheidole sp. E1 (Group E)	Generalised Myrmicinae	3	6	end	T	Qld
Pheidole sp. E2 (Group E)	Generalised Myrmicinae	7	42	end	na	na
Pheidole sp. F1 (Group F)	Generalised Myrmicinae	2	6	end	T	Qld
Pheidole sp. O1 (*onifera* gp.)	Generalised Myrmicinae	7	19	end	T	na
Pheidole sp. V1 (*variabilis* gp.)	Generalised Myrmicinae	0	0	end	W	Qld
Podomyrma laevifrons	Tropical Climate Specialist	0	0	Indo	T	Qld
Solenopsis sp. A	Cryptic species	6	43	end	W	Qld
Solenopsis sp. B	Cryptic species	0	0	end	T	Qld
*Tetramorium bicarinatum**	Opportunist	0	0	W	T	W
Tetramorium lanuginosum	Opportunist	2	4	end	T	W
*Tetramorium simillimum**	Opportunist	7	28	W	T	W
Tetramorium sp. A (*striolatum* gp.)	Opportunist	1	2	end	E	Qld
Tetramorium sp. B (*ornatum* gp.)	Opportunist	1	1	end	T	na
Tetramorium sp. C (*ornatum* gp.)	Opportunist	0	0	end	T	na
Tetramorium (*Rhoptromyrmex*) sp.	Opportunist	0	0	end	na	na
Dolichoderinae						
Iridomyrmex sanguineus	Dominant Dolichoderinae	0	0	end	W	W
Iridomyrmex suchieri	Dominant Dolichoderinae	4	22	end	W	W
Iridomyrmex tenuiceps	Dominant Dolichoderinae	1	1	end	E	W
Iridomyrmex sp. A (*mjobergi* gp.)	Dominant Dolichoderinae	0	0	end	E	W
Iridomyrmex sp. anc1 (*anceps* complex)	Dominant Dolichoderinae	4	29	end	T	na
Iridomyrmex sp. anc2 (*anceps* complex)	Dominant Dolichoderinae	3	14	end	T	na
Iridomyrmex sp. anc3 (*anceps* complex)	Dominant Dolichoderinae	6	30	end	T	na
Iridomyrmex sp. pal1 (*pallidus* gp.)	Dominant Dolichoderinae	0	0	end	E	na
Iridomyrmex sp. pal2 (*pallidus* gp.)	Dominant Dolichoderinae	0	0	end	E	na
Leptomyrmex ruficeps	Tropical Climate Specialist	0	0	end	T	Qld
Leptomymrex rufipes	Tropical Climate Specialist	1	1	end	T	W
Ochetellus sp. A (*glaber* gp.)	Opportunist	2	4	end	W	Qld
Ochetellus sp. B (*glaber* gp.)	Opportunist	1	1	end	na	na
Papyrius sp. 1 (*nitidus* gp.)	Dominant Dolichoderinae	0	0	end	W	W
*Tapinoma melanocephalum**	Opportunist	0	0	W	T	W
Tapinoma sp. A	Opportunist	1	1	end	W	Qld
Tapinoma sp. B	Opportunist	0	0	end	W	Qld
Formicinae						
Camponotus confusus	Subordinate Camponotini	0	0	end	T	W
Camponotus 'crozieri'	Subordinate Camponotini	0	0	end	T	W
Camponotus rubiginosus	Subordinate Camponotini	0	0	end	T	Qld
Camponotus sp. A (*novaehollandiae* gp.)	Subordinate Camponotini	3	4	end	T	na
Camponotus sp. B (nr. *novaehollandiae* gp.)	Subordinate Camponotini	2	4	end	na	na
Camponotus sp. C (*ephippium* gp.)	Subordinate Camponotini	0	0	end	na	na
Colobopsis vitrea	Subordinate Camponotini	0	0	Indo	T	W
Melophorus sp. B (*curtus* gp.)	Hot-Climate Specialist	4	14	end	W	na
Melophorus sp. lud1 (*ludius* gp.)	Hot-Climate Specialist	4	12	end	E	na
Melophorus sp. A (*pillipes* gp.)	Hot-Climate Specialist	3	24	end	E	na
Melophorus sp. B (*pillipes* gp.)	Hot-Climate Specialist	0	0	end	E	na
Melophorus sp. A (*rufoniger* gp.)	Hot-Climate Specialist	1	1	end	W	na
Melophorus sp. S1 (*sulla* gp.)	Hot-Climate Specialist	1	1	end	E	na
Nylanderia glabrior	Opportunist	7	23	Indo	W	W
Nylanderia sp. A (*obscura* gp.)	Opportunist	2	2	end	na	na

Appendix 1 continued

Sub-family and species	Functional group	N sites	N traps	Distr1	Distr2	Distr3
Oecophylla smaragdina	Tropical Climate Specialist	6	30	pan	T	W
Opisthopsis haddoni	Subordinate Camponotini	0	0	end	T	W
Opisthopsis linnaei	Subordinate Camponotini	0	0	Indo	T	Qld
Paraparatrechina sp. A (*minutula* gp.)	Opportunist	0	0	end	na	na
*Paratrechina longicornis**	Opportunist	6	28	W	W	W
Plagiolepis sp. (exigua gp.)	Cryptic species	0	0	end	na	na
Polyrhachis clotho	Subordinate Camponotini	0	0	end	T	W
Polyrhachis cupreata	Subordinate Camponotini	0	0	end	T	Qld
Polyrhachis daemeli	Subordinate Camponotini	0	0	end	T	Qld
Polyrhachis delecta	Subordinate Camponotini	0	0	end	T	rf
Polyrhachis dives	Subordinate Camponotini	0	0	Indo	T	W
Polyrhachis nr. *dorowi*	Subordinate Camponotini	0	0	end	T	na
Polyrhachis elegantula	Subordinate Camponotini	0	0	end	T	Qld
Polyrhachis lata	Subordinate Camponotini	0	0	end	T	Qld
Polyrhachis monteithi	Subordinate Camponotini	0	0	end	T	Qld
Polyrhachis nr. *monteithi*	Subordinate Camponotini	0	0	end	T	na
Polyrhachis robsoni	Subordinate Camponotini	0	0	end	T	Qld
Polyrhachis senilis	Subordinate Camponotini	0	0	end	T	W
Polyrhachis tubifera	Subordinate Camponotini	1	1	end	T	Qld
Polyrhachis sp. 9 (*obtusa* gp.)	Subordinate Camponotini	0	0	end	T	W
Polyrhachis sp. (*inconspicua* gp.)	Subordinate Camponotini	0	0	end	T	na
Polyrhachis sp. (*Hedomyrma* subgenus)	Subordinate Camponotini	0	0	end	T	na