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ORIGINAL PAPER

Exploring a new biodiversity frontier: subterranean ants in northern Australia

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Abstract Although it is common for ant surveys to uncover previously uncollected species, a recent study of subterranean ants in Amazonian Ecuador has indicated that an *entire ant fauna* may remain largely undiscovered. Here we report on the first systematic investigation of subterranean ants in northern Australia, in order to assess the extent to which the high abundance and diversity of subterranean ants in Amazonia is apparent in tropical Australia. We use a novel sampling technique that combines elements of an attractant bait and a pitfall trap, and allows many traps to be deployed simultaneously. Our main study was conducted at three closely approximated sites in Darwin, where the local ant fauna has been intensively surveyed using conventional (above-ground) sampling techniques. The 720 traps deployed resulted in 421 species records, representing 29 species from 17 genera. Sixteen of these species have cryptobiotic morphology, with four recorded here for the first time. Remarkably, one of these four (a blind species of *Solenopsis*) was the second most frequently caught species in subterranean traps, with 70 records. Ant abundance, species richness and composition varied markedly between sites, despite site similarity in soils and vegetation. Total ant records were greater in the middle compared with start of the wet season, declined with depth, and were greater after 4 days than one. Sampling at six sites in the Mitchell Falls area of the northern Kimberley region, 1,200 km southwest of Darwin, also revealed several cryptobiotic species new to science, including a new genus record (*Pseudolasius*) for Western Australia. Our underground sampling has therefore revealed an abundant and diverse subterranean ant fauna in northern Australia, containing many cryptobiotic species not previously collected. We use our results to provide methodological guidelines for most effectively sampling this fauna. Combined with the Amazonian study, our findings indicate that a specialist subterranean ant fauna,

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including numerous species remaining to be discovered, might be a feature of tropical landscapes throughout the world.

Keywords Ant biodiversity · Australia · New species · Savanna · Subterranean pitfall traps

Introduction

Ants are one of the most familiar groups of insects; they play dominant ecological roles in terms of biomass, energy and nutrient flows (Hölldobler and Wilson 1990; Folagarait 1998), have many important interactions with plants (Buckley 1982; Beattie 1985; Huxley and Cutler 1991), and are widely used as bio-indicators in ecological monitoring (Andersen and Majer 2004). However, outside of Europe and North America, the majority of ant species remain undescribed, and it is routine for ant surveys to uncover previously uncollected species. This is especially the case in Australia, where only one-fifth of the estimated 6,500 species have been described (Andersen 2007).

A recent study in Amazonian Ecuador (Wilkie et al. 2007) indicated that our knowledge of the world's ant fauna might be more incomplete than previously thought—it is possible that an *entire ant fauna* remains largely undiscovered. It has long been acknowledged that conventional ant survey techniques under-sample species foraging within soil (Longino and Colwell 1997; Fowler et al. 2000; Lubertazzi and Tschinkel 2003), but the Wilkie et al. (2007) study has revealed for the first time the remarkable diversity of specialist subterranean species. Nearly 20% of the 47 species they collected in specially designed subterranean probes were not recorded using conventional above-ground sampling techniques in the same area, and at least two of these subterranean specialists were new to science. Ant diversity was highest within the top 12.5 cm of the soil profile, where 42 of the 47 species were collected (including most of the epigaeic species), and all the specialist subterranean species were found in the top 25 cm.

As far as we are aware, the Wilkie et al. (2007) study remains the only systematic investigation of a subterranean ant fauna. Here we describe the subterranean ant faunas of two locations in northern Australia, in order to assess the extent to which the level of subterranean ant abundance and diversity in Amazonia is apparent in tropical Australia. Our primary aim is to examine the extent to which ants collected underground in northern Australia represent specialist subterranean species that have hitherto been unrecorded. We also document variation in subterranean catches with soil depth, season and period of sampling, to help with the development of protocols for effectively sampling subterranean ants in the seasonal tropics.

Methods

Study sites

The main study was conducted in the grounds of CSIRO's Tropical Ecosystems Research Centre (TERC) in Darwin (12°25′S, 130°53′E), Northern Territory, with additional sampling in the Mitchell Falls (14°48′S, 125°41′) area of the northern Kimberley region of Western Australia, 1,200 km southwest of Darwin. Both regions experience a tropical monsoonal climate, with rainfall (annual means of about 1,700 mm in Darwin and

1,500 mm at Mitchell Falls) restricted to a summer wet season, and temperatures being high (mean daily maxima >30°C) throughout the year.

At TERC, subterranean ants were sampled at three sites, each separated by about 200 m. The vegetation at all sites was open forest dominated by *Eucalyptus tetrodonta* and *E. miniata*, on brown lateritic soil. In contrast to the surrounding savanna landscape, the sites had been rarely burnt over the past 30 years, and grasses were very sparse due to enhanced woody cover (see Woinarski et al. 2004). Ants have been extensively collected at TERC over the past two decades using a range of conventional above-ground techniques (hand collecting, baiting, pitfall trapping, litter extractions), with more than 100 species recorded (A. N. Andersen, unpublished data). There have also been extensive surveys of ants using conventional techniques in the broader Darwin region (Andersen and Patel 1994; Andersen and Reichel 1994; Andersen et al. 2006; Parr and Andersen 2008).

The Mitchell Falls region is dominated by two landforms: the lateritic Mitchell Plateau, supporting eucalypt-dominated open forest on red loams; and sandstone outcrops and associated sandy soils around the base of the plateau, supporting eucalypt-dominated woodland and shrubland. Subterranean ants were sampled at six sites, three each on sandy (S1—14.839°S 125.715°E; S2—14.874°S 125.748°E; S3—14.711°S 125.788°E) and lateritic (L1—14.800°S 125.789°E; L2—14.7544°S 125.788°E; L3—14.7540°S 125.788°E) soils, with sites separated by between 100 m and 20 km. They were a subset of 16 sites intensively sampled during June and July 2007 using pitfall traps, which recorded 165 species from 33 genera (Andersen et al. 2010). The savanna ant fauna of other areas of the northern Kimberley region is not well known, but the ants of rainforest patches have been systematically surveyed (Andersen and Majer 1991; Andersen 1992).

Subterranean traps

Ants were sampled utilising subterranean traps similar to those used by Yamaguchi and Hasegawa (1996) to assess rates of subterranean predation by ants, and subsequently by Lubertazzi and Tschinkel (2003) to sample subterranean ants in Florida. They also have several features in common with the subterranean traps described by Schmidt and Solar (2010). Such traps are far simpler than the cylindrical probes used by Wilkie et al. 2007; in our case hundreds can readily be deployed simultaneously. The traps were capped plastic vials 4 cm high and 1 cm in diameter, with four holes (2 mm diameter) drilled in the upper half to allow access by ants. To attract ants, a mixture of honey, peanut butter and fish paste was smeared on the inner walls above the access holes using a fine paint brush. The traps were half-filled with an ethanol/ethylene glycol mix in order to retain and preserve ants that fell to the bottom of the trap. This allows for the capture of all species visiting traps, including behaviourally submissive ants that might be displaced from baits by dominant species (cf. Wilkie et al. 2007). At the Darwin site, traps were inserted into holes drilled into the soil using a hand-held augur, and covered with soil. At Mitchell Falls, holes were made by hammering a metal stake into the soil. A length of string or wire extending above the soil surface was attached to each trap, to facilitate trap re-location after burial.

Sampling

At the three TERC sites in Darwin, traps were deployed during different months (from 24 November 2008, corresponding to the beginning of the wet season; and from 12 January 2009, corresponding to the middle of the wet season), at different depths (5, 10 and 15 cm), and for different durations (1 and 4 days). At each site and month, sampling was conducted at 20 locations, spaced by 2 m along a 38 m transect. At each location, six traps were deployed, corresponding to the six combinations of depth (×3) and sampling duration (×2), resulting in 120 traps per site per occasion for a total of 720 traps.

At the Mitchell Falls sites, traps were deployed on a single occasion (mid February 2009) at a single depth (20 cm) for a single duration (2 days). Twenty traps were deployed at each site, arranged in two parallel transects of 10 traps with 5 m spacing, with transects separated by 50 m.

Analysis

All ants were sorted to species, and where possible named (see Shattuck (1999) for species authorities). Species that could not be confidently named were assigned to species groups following Andersen (2000), and given number codes (sp. 1, sp. 2, etc.) that follow and extend those used in previous studies of ants in the Top End of the Northern Territory (Andersen and Patel 1994; Andersen and Reichel 1994; Andersen et al. 2006; Parr and Andersen 2008). Species from Mitchell Falls that did not match known Top End species were assigned letter codes (sp. A., sp. B, etc.) that apply to this study only.

The extent to which species collected in traps are subterranean specialists was examined by comparison with their records from conventional (above-ground) sampling techniques in the respective regions (see 'Study sites' section), and through reference to the CSIRO TERC ant collection in Darwin, which contains the most comprehensive collection of northern Australian ants.

The effects of site, month of sampling, depth of burial and sampling duration on ant catches in Darwin were analysed by 4-way nested ANOVA, with site as a random factor and month, depth and duration as fixed factors nested within site, using the R-package v.2.6.0 (R-Development Core Team 2007). The unit of analysis was a sample of 20 traps, and variables examined were total ant records (each species occurrence in a trap represents a record), species richness, and the frequency of occurrence of each common species (those with a total of 20 or more occurrences).

Results

Darwin

There was a total of 421 species records from the 720 traps deployed at TERC, representing 29 species from 17 genera (Table 1). Ant abundance was often extremely high, with more than one hundred individuals frequently recorded in a single trap. The most common species were *Pheidole* sp. 8 (89 records), *Solenopsis* sp. 10 (70), *Solenopsis* sp. 1 (61), *Tetramorium simillimum* (28), *Pheidole* sp. 30 (25), *Cerapachys edentatus* (23), and *Pheidole* sp. 26 (20).

Nearly half (13) of the species were epigaeic ants that are common throughout the Darwin region: *Bothroponera* sp. 1, *Odontomachus* sp. nr. *turneri, Crematogaster* sp. 2*, Meranoplus* sp. 13*, Monomorium donisthorpei, M. floricola, M. ?nigrius, Monomorium* sp. 24, *Pheidole* sp. 14, *Tetramorium* sp. 1, *T. simillimum, T. lanuginosum* and *Paratrechina* sp. 4. The remaining 16 species have cryptobiotic morphology, with small body size, short legs, and tiny or absent eyes. Based on TERC ant collection records, twelve of these have been recorded relatively frequently in the region from the soil-litter interface: *Cerapachys edentatus*, *Ectomomyrmex ruficornis, Hypoponera* sp. 1*, Carebara* sp. 1, *Machomyrma*

Table 1 Ants collected in subterranean traps at TERC, showing variation between sampling months, sites, soil depth and duration traps were left out

	Month		Site			Depth			Duration		Total
	Nov	Jan	1	2	3	5 cm	10 cm	15 cm	1 day	4 days	
Subfamily Cerapachyinae											
Cerapachys edentatus	10	13	9	14		6	6	11	5	18	**23**
Sphinctomyrmex sp. 6		3	1	2		1	1	1		3	**3**
Subfamily Ponerinae											
Bothroponera sp. 1 (*porcata* gp.)	1	3	3	1		3	1		1	3	**4**
Ectomomyrmex ruficornis	3			2	1	3			1	2	**3**
Hypoponera sp. 1	2	1	3			2	1			3	**3**
Odontomacus sp. nr. *turneri*	2	4	4		2	3	1	2	2	4	**6**
Subfamily Myrmicinae											
Carebara sp. 1	7		4	3		1	2	4	4	3	**7**
Crematogaster sp. 2 (*australis* complex)	1			1		1			1		**1**
Machomyrma ?dispar	6		6			2	2	2	4	2	**6**
Meranoplus sp. 13 (*aureolus* complex)		1		1		1			1		**1**
Monomorium donisthorpei	1	2		2	1	3			3		**3**
*M. floricola**		1		1		1				1	**1**
M. ?nigrius	1	1		2		1	1		2		**2**
Monomorium sp. 24 (*laeve* gp.)	2	3	5			3	1	1	4	1	**5**
Monomorium sp. 48 (*fossulatum* gp.)	1		1					1	1		**1**
Pheidole sp. 8 (Group F)	27	62	34	31	24	44	24	21	37	52	**89**
Pheidole sp. 14 (*ampla* gp.)	1	1		2		1		1		2	**2**
Pheidole sp. 26 (Group F)	6	14	15	5		10	9	1	12	8	**20**
Pheidole sp. 30 (Group F)	11	14	24	1		12	8	5	14	11	**25**
Solenopsis sp. 1	32	29	38	14	9	21	23	17	26	35	**61**
Solenopsis sp. 9	8	10	2	13	3	8	3	7	7	11	**18**
Solenopsis sp. 10	28	42	19	45	6	21	27	22	18	52	**70**
Solenopsis sp. 11	1	2	1	1	1	3				3	**3**
Strumigenys sp. nr. *sutrix*	2			1	1	2			1	1	**2**
*Tetramorium simillimum**	10	18	4		24	16	5	7	12	16	**28**
Tetramorium lanuginosum	2	5		1	6	5	1	1	4	3	**7**
Tetramorium sp. 1 (*striolatum* gp.)		7		7		6		1	5	2	**7**
Subfamily Dolichoderinae											
Arnoldius sp. 1	1	4	5				3	2	2	3	**5**
Subfamily Formicinae											
Paratrechina sp. 4 (*vaga* gp.)	2	13	12	3		6	2	7	8	7	**15**
Total	**168**	**253**	**190**	**153**	**78**	**186**	**121**	**114**	**175**	**246**	**421**
No. Species	**25**	**23**	**19**	**22**	**11**	**27**	**19**	**19**	**24**	**24**	**29**

Data are frequency of occurrence in traps (n = 360 for each month and duration; n = 240 for each site and depth; with total n = 720)

* Introduced species

Table 2 ANOVA *P*-values for the main effects of site, month, depth and sampling duration on total ant records, species richness, and the frequency of occurrence of the seven most frequently recorded species

	Site	Month	Depth	Duration
Total records	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Mean species richness	**<0.001**	0.060	**<0.001**	**0.006**
Pheidole sp. 8	0.354	0.354	**0.006**	0.093
Solenopsis sp. 10	**<0.001**	**0.043**	**0.043**	**0.043**
Solenopsis sp. 1	**<0.001**	0.578	0.387	0.105
Tetramorium simillimum	**<0.001**	**0.037**	**0.003**	0.277
Pheidole sp. 30	**<0.001**	0.617	0.365	0.617
Cerapachys edentatus	**0.007**	0.546	0.368	**0.015**
Pheidole sp. 26	**<0.001**	**0.037**	**0.011**	0.277

There were significant interactions between site and depth for *Solenopsis* sp. 10 and *Pheidole* sp. 26, between site and duration for *Solenopsis* sp. 10, and between site and month for *Solenopsis* sp. 10, *Cerapachys edentatus* and *Tetramorium simillimum*. Significant values ($P < 0.05$) are shown in bold

?*dispar*, *Monomorium* sp. 48, *Pheidole* sp. 8, *Pheidole* sp. 26, *Solenopsis* sp. 1, *Solenopsis* sp. 9, *Strumigenys* sp. nr. *sutrix* and *Arnoldius* sp. 1. The remaining four species are not represented in the TERC collection: *Pheidole* sp. 30, *Sphinctomyrmex* sp. 6, *Solenopsis* sp. 10 and *Solenopsis* sp. 11. Remarkably, one of these (*Solenopsis* sp. 10) was the second most frequently caught species in subterranean traps, with 70 records (Table 1).

Total ant records varied significantly between sites, month of sampling, soil depth and sampling duration (Table 2). Total ant records varied from 78 at site 3 to 190 at site 1, was higher in January (253) than November (168), declined with depth (from 186 at 5 cm to 114 at 15 cm), and was higher after 4 days (246) than one (175) (Table 1). Species richness varied significantly between sites, declined significantly with soil depth (27 at 5 cm, compared with 19 at 10 cm and 15 cm), but did not vary significantly with month (Tables 1, 2). Mean ($n = 18$) species richness was significantly higher after 4 days duration (6.5) compared with 1 day (5.2; $P = 0.006$), but overall species richness was the same (24) for both. The frequency of occurrence of six of the seven most abundant species also varied significantly between sites (Table 2), with *Cerapachys edentatus*, *Pheidole* sp. 26 and *Pheidole* sp. 30 all occurring at sites 1 and 2 but not 3, and *Solenopsis* sp. 10 being most common at, and *Tetramorium simillimum* absent from, site 2 (Table 1). Of the seven most common species, three varied significantly with month, four with depth, and two with sampling duration (Table 2).

Mitchell falls

In total, there were 110 species records from the 120 traps deployed in the Mitchell Falls region, representing 15 species from eight genera (Table 3). The sandstone sites yielded 12 species from 40 species records, compared with only seven species from 70 records from the laterite sites. None of the species occurred in TERC samples, although five (*Pheidole* sp. 3, *Pheidologeton affinis*, *Solenopsis* sp. 13, *Tetramorium* sp. 2 and *Paratrechina* sp. 4) occur in the Darwin region (TERC ant collection records). Seven (47%) of the 15 species were not recorded during extensive pitfall trapping at the same sites and elsewhere in the Mitchell Falls region (Andersen et al. 2010). Four of these have cryptobiotic morphology: *Carebara* sp. A, *Pheidole* sp. G, *Solenopsis* sp. A and *Solenopsis* sp. C. Despite not being

Table 3 Frequency of occurrence of ant species recorded in subterranean traps in the Mitchell Falls region, at sandstone (S1–S3) and laterite (L1–L3) sites

	S1	S2	S3	L1	L2	L3	TOTAL
Myrmicinae							
Aphaenogaster kimberleyensis				6			**6**
Carebara sp. A*			1		2	1	**4**
Pheidole sp. 3 (*variabilis* gp.)	2	1	1				**4**
Pheidole sp. B (*ampla* gp.)*			1				**1**
Pheidole sp. C (Group C)			1				**1**
Pheidole sp. 1 (*mjobergi* gp.)		2					**2**
Pheidole sp. E (Group B)*		4					**4**
Pheidole sp. G (Group F)*				8			**8**
Pheidologeton affinis				2	2		**4**
Solenopsis sp. A*	1	2	6			1	**10**
Solenopsis sp. 13		5	6	7	11	12	**41**
Solenopsis sp. C*	3		1	1	11	6	**22**
Tetramorium sp. 2 (*striolatum* gp.)			1				**1**
Formicinae							
Pseudolasius sp. A*	1						**1**
Paratrechina sp. 4 (*vaga* gp.)			1				**1**
Total	**7**	**14**	**19**	**24**	**26**	**20**	**110**
No. species	**4**	**5**	**9**	**5**	**4**	**4**	**15**

Species not recorded during extensive pitfall trapping at the same sites and elsewhere in the Mitchell Falls region (Andersen et al. 2010) are indicated by an asterisk

recorded in previous pitfall trapping, the two species of *Solenopsis* were among the most common and widespread ants collected in subterranean traps. However, the most noteworthy record in subterranean traps was *Pseudolasius* sp. A, as this genus was previously known in Australia only from rainforest in North Queensland and sub-coastal Northern Territory (Shattuck 1999).

Discussion

This study is the first systematic investigation of subterranean ants in Australia, using a novel technique that combines elements of an attractant bait and a pitfall trap. It has revealed a diverse and abundant subterranean ant fauna in northern Australia, with several species recorded for the first time, and mirrors results from subterranean sampling in Amazonia.

A species collected in our traps may be considered to be a subterranean specialist if it: (i) has typical cryptobiotic morphology (small body size, short legs, and tiny or absent eyes); (ii) was disproportionately abundant in subterranean samples compared with existing records from conventional (above-ground) sampling techniques; and, for the Darwin study, (iii) occurred most frequently at depths below 5 cm. Nearly half (13) of the 29 species recorded in subterranean traps in Darwin do not have cryptobiotic morphology (i.e. are epigaeic species), and they were mostly recorded at the shallowest depth (5 cm). The majority of the remaining 16 cryptobiotic species have previously been collected at the soil/litter interface throughout the broader Darwin region, but, based on records in the

TERC ant collection, four of the species have never before been recorded. Of the ten cryptobiotic species occurring in five or more traps, five (*Cerapachys edentatus*, *Carebara* sp. 1, *Solenopsis* sp. 1, *Solenopsis* sp. 10 and *Arnoldius* sp.1) had peak abundances below 5 cm, and so may be considered subterranean specialists. Remarkably, although *Solenopsis* sp. 10 had never been recorded prior to this study, it was common in subterranean traps at all three TERC sites and was the second most abundant species overall. It therefore appears to forage exclusively underground.

Total ant records, species richness and species composition all varied significantly between sites at TERC. Such patchiness at closely approximated sites with similar soils and vegetation suggests that subterranean species have high rates of spatial turnover. Given that each site had at least two 'unique' species, and that one site (site 2) had nine, it is highly likely that additional subterranean species occur in the immediate region.

Fewer species were collected in subterranean traps in the Mitchell Falls region (15) compared with Darwin (29), but this can be attributed to the far lower sampling effort at Mitchell Falls. The ratio of total species records to total traps was actually higher at Mitchell Falls (0.92) than Darwin (0.58). Both regions therefore have a diverse and abundant subterranean ant fauna. Nearly half of the species collected in subterranean traps in the Mitchell Falls region had not been recorded in pitfall traps at the same sites or elsewhere in the region (Andersen et al. 2010), and are not represented in the TERC collection. They included two blind species of *Solenopsis* that were among the most frequently recorded ants, and so are very likely subterranean specialists. These two species are closely related to three blind species of *Solenopsis* recorded in Darwin (*Solenopsis* spp. 9–11), two of which were likewise common but never before recorded. This points to the existence of a diverse and abundant group of blind, specialist subterranean species of *Solenopsis* from tropical Australia that has hitherto been largely unknown.

The use of subterranean traps has also revealed a new genus record for Western Australia in *Pseudolasius*. The species is almost certainly new, and its sandstone open habitat is in striking contrast to the rainforests that its congeners are associated with elsewhere in Australia and the broader South-East Asian region. Its eyes are extremely small, which is suggestive of a subterranean habit: it is possibly a honeydew specialist associated with underground Hemiptera, as are species of other cryptobiotic formicine genera such as *Acanthomyops* and *Acropyga* (Way 1963).

Our mixture of honey, peanut butter and fish paste is unlikely to attract specialist predators such as species of *Leptanilla* (López et al. 1994). However, the results presented here demonstrate that the traps used are a simple but effective way of sampling the subterranean ant fauna with generalised feeding habits. Results from Darwin provide guidelines on their most effective use. Catches were higher in the middle than start of the wet season, and this is likely to be the optimal time for sampling (assuming lower catches during the dry season). Catches were highest at 5 cm depth, but here there was very substantial 'contamination' by epigaeic species; if the focus is on subterranean specialists then 10 cm depth would seem ideal. Total species richness after 4 days of sampling was not significantly higher than after than one, indicating that with sufficient traps a single day is adequate for obtaining an effective sample.

Conclusion

Our study has revealed an abundant and diverse subterranean ant fauna in northern Australia, containing many cryptobiotic species not previously collected. These species have high spatial turnover, at both local and regional scales, suggesting that many additional subterranean species occur across Australia's vast tropical savanna landscapes. Combined with the Amazonian study (Wilkie et al. 2007), our findings indicate that a specialist subterranean ant fauna, including numerous species remaining to be discovered, might be a feature of tropical landscapes throughout the world.

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References

Andersen AN (1992) The rainforest ant fauna of the northern Kimberley region of Western Australia (Hymenoptera: Formicidae). J Aust Ent Soc 31:187–192

Andersen AN (2000) The ants of northern Australia: a guide to the monsoonal fauna. CSIRO Publishing, Collingwood

Andersen AN (2007) Ant diversity in arid Australia: a systematic overview. In: Snelling RR, Fisher BL, Ward PS (eds) Advances in ant (Hymenoptera: Formicidae) systematics: homage to E. O. Wilson—50 years of contributions, vol 80. Memoirs of the American Entomological Institute, Gainesville, FL, pp 19–51

Andersen AN, Majer JD (1991) The structure and biogeography of rainforest ant communities in the Kimberley region of northwestern Australia. In: McKenzie NL, Johnston RB, Kendrick PJ (eds) Kimberley rainforests of Australia. Surrey Beattie & Sons, Sydney, pp 333–346

Andersen AN, Majer JD (2004) Using invertebrates as bioindicators in land management: ants show the way Down-Under. Front Ecol Environ 2:291–298

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, Reichel H (1994) The ant fauna of Holmes Jungle, a rainforest patch in the seasonal tropics of Australia's Northern Territory. J Aust Ent Soc 33:53–58

Andersen AN, Hertog T, Woinarski JCZ (2006) Long-term fire exclusion and ant community structure in an Australian tropical savanna: congruence with vegetation succession. J Biogeogr 33:823–832

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. J Insect Conserv. doi:10.1007/s10841-010-9294-2

Beattie AJ (1985) The evolutionary ecology of ant-plant mutualisms. Cambridge University Press, Cambridge

Buckley RC (1982) Ant-plant interactions in Australia. Junk Press, The Hague

Folagarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. Biodivers Conserv 7:1221–1244

Fowler HG, Delabie JHC, Moutinho PRS (2000) Hypogaeic and epigaeic ant (Hymenoptera: Formicidae) assemblages of Atlantic coastal rainforest and dry mature and secondary Amazon forest in Brazil: continuums or communities. Trop Ecol 41:73–80

Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge, Massachusetts

Huxley CR, Cutler DF (eds) (1991) Ant-plant interactions. Oxford University Press, Oxford

Longino JT, Colwell RK (1997) Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. Ecol Appl 7:1263–1277

López F, Martínez MD, Barandica JM (1994) Four new species of the genus *Leptanilla* (Hymenoptera: Formicidae) from Spain—relationships to other species and ecological issues. Sociobiology 24:179–212

Lubertazzi D, Tschinkel WR (2003) Ant community change across a ground vegetation gradient in north Florida's longleaf pine flatwoods. J Insect Sci 3:21

Parr CL, Andersen AN (2008) Fire resilience of ant assemblages in long-unburnt savanna. Aust Ecol 33:830–838

R-Development Core Team (2007) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna

Schmidt FA, Solar RRC (2010) Hypogaeic pitfall traps: methodological advances and remarks to improve the sampling of a hidden ant fauna. Insect Soc (in press)

Shattuck SO (1999) Australian ants: their biology and identification. CSIRO Publishing, Collingwood

Way MJ (1963) Mutualism between ants and honeydew-producing Homoptera. Ann Rev Entomol 8:301–344

Wilkie KTR, Mertl AL, Tranello JFA (2007) Biodiversity below ground: probing the subterranean ant fauna of Amazonia. Naturwissenschaften 94:725–731

Woinarski JCZ, Risler J, Kean L (2004) Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical *Eucalyptus* open forest, Northern Territory, Australia. Aust Ecol 29:156–176

Yamaguchi T, Hasegawa M (1996) An experiment on ant predation in soil using a new bait trap method. Ecol Res 11:11–16