RAINFOREST ANTS (HYMENOPTERA: FORMICIDAE) ALONG AN ELEVATIONAL GRADIENT AT EUNGELLA IN THE CLARKE RANGE, CENTRAL QUEENSLAND COAST, AUSTRALIA

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Here we provide a faunistic overview of the rainforest ant fauna of the Eungella region, located in the southern part of the Clarke Range in the Central Queensland Coast, Australia, based on systematic surveys spanning an elevational gradient from 200 to 1200 m asl. Ants were collected from a total of 34 sites located within bands of elevation of approximately 200, 400, 600, 800, 1000 and 1200 m asl. Surveys were conducted in March 2013 (20 sites), November 2013 and March–April 2014 (24 sites each), and ants were sampled using five methods: pitfall traps, leaf litter extracts, Malaise traps, spraying tree trunks with pyrethroid insecticide, and timed bouts of hand collecting during the day. In total we recorded 142 ant species (described species and morphospecies) from our systematic sampling and observed an additional species, the green tree ant *Oecophylla smaragdina*, at the lowest elevations but not on our survey sites. With the caveat of less sampling intensity at the lowest and highest elevations, species richness peaked at 600 m asl (89 species), declined monotonically with increasing and decreasing elevation, and was lowest at 1200 m asl (33 spp.). Ant species composition progressively changed with increasing elevation, but there appeared to be two gradients of change, one from 200–600 m asl and another from 800 to 1200 m asl. Differences between the lowland and upland faunas may be driven in part by a greater representation of tropical and arboreal-nesting species in the lowlands and a greater representation of subtropical species in the highlands. We briefly overview the Eungella ant fauna of each subfamily and make comparisons with ants collected from surveys along comparable elevational gradients at Lamington National Park in subtropical south-eastern Queensland, and Mt Lewis in the Wet Tropics bioregion of northern Queensland.

Keywords: ants, Formicidae, Eungella

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INTRODUCTION

As part of a broader research program investigating the distributions of rainforest invertebrates and plants along gradients of elevation in eastern Queensland, we sampled ants in the rainforests of the Eungella region, referred to as Eungella hereafter. Located about 60–70 km west of the city of Mackay, Eungella is situated within the Central Queensland Coast (CQC), the region extending from just north of the town of Proserpine to south of Sarina. The rainforests of the CQC are biogeographically isolated from the rainforests of the Wet Tropics region to the north by the Burdekin-Lynd Barrier, a corridor of low-elevation, drier forests. Similarly, another biogeographic barrier to the south, the St Lawrence Gap, separates the rainforests of the CQC from a chain of subtropical rainforest patches in south-eastern Queensland and north-eastern New South Wales. The Clarke Range contains the greatest extent of upland rainforests in the CQC, and the highest-elevation rainforests occur in the Eungella region in the southern Clarke Range.

There has been no published overview of the ant fauna of Eungella, but information on the ant species of the region is scattered throughout the taxonomic literature. It was not our intention to review comprehensively this literature for records of species from Eungella. However, the significance of the ant fauna of the region's upland rainforests is apparent since it contains both endemic species (Ogata & Taylor, 1991) and disjunct populations of more southerly species

(e.g. see Taylor, 1977; Shattuck, 2015). Instead, here we provide an overview of Eungella's fauna of rainforest ants based on extensive surveys at 34 sites spanning an elevational gradient encompassing almost the entire extent of rainforest in the region, from 200 to 1200 m above sea level. We also compare the ants collected from our Eungella gradient with collections of ants made along similar elevational gradients in the sub-tropical rainforests of south-eastern Queensland and the tropical rainforests of the Wet Tropics bioregion of far northern Queensland.

METHODS

Study Design

We sampled ants from rainforests in the Eungella region (21.1°S) from sites spanning a gradient of elevation from 200 to 1200 m above sea level (asl). Four to seven sites were established within bands of elevation separated by around 200 vertical metres. Owing to the difficulties of working in mountainous terrain and locating suitable habitat, the elevations of sites within each band varied. The mean elevation of sites within each band, however, was always within ±10 vertical metres of the desired elevation. An average decrease of 0.6°C per 100 m increase in elevation occurred along the Eungella transect, based on data collected in December 2014 to February 2015 using iButtons™.

Ant sampling was conducted on three separate survey periods: 4–26 March 2013, 4–30 November 2014, and 15 March–12 April 2014. In March 2013, ants were sampled from five sites in each of four bands of elevation: approximately 400, 600, 800 and 1000 m asl. All sites were within Eungella National Park. Sites at 400 and 600 m asl were situated close to Finch Hatton Gorge, sites at 800 m asl were along the road between Eungella township and Broken River in the vicinity of the Sky Window Picnic Area, and sites at 1000 m asl were located along the Mt Dalrymple Road and the beginning of the walking track to Mt Dalrymple. In November 2013 and March to April 2014, ants were sampled from four sites in each of six bands of elevation: approximately 200, 400, 600, 800, 1000 and 1200 m asl. These two later surveys re-sampled four of the five sites at 1000 m asl established in March 2013. Due to the close proximity of some sites established at 400, 600 and 800 m asl (closest distance between sites was 100 m, 90 m and 190 m, respectively) in March 2013, only two of the five sites at each elevation were re-sampled in the two later surveys. Instead, two new sites were established at each of 400 and 600 m asl near Owens Creek in Pelion State Forest, as were new sites at 800 m asl along Diggings Road and Dalrymple Road. In addition, four sites at 200 m asl, one at Finch Hatton Gorge and three along Owens Creek in Pelion State Forest, were sampled, as were four sites at 1200 m asl: two on or close to Mt William, one on Mt Dalrymple and another along the walking track to Mt Dalrymple, all in Eungella National Park. Thus, in total, four unique sites were sampled at 200 and 1200 m asl, five sites at 1000 m asl, and seven at 400, 600, and 800 m asl (Table 1). Individual sites were sampled one, two or three times, as indicated in Table 1. As a result, there was variation among elevational bands in the total number of site surveys (the product of the number of unique sites and how often each was surveyed): 200 m asl and 1200 m asl, eight total site surveys; 400, 600, 800 and 1000 m asl, 13 site surveys.

TABLE 1. Summary of actual elevations and latitude and longitude co-ordinates of Eungella survey sites arranged by elevational bands. Also indicated are which sites were sampled in the three survey periods: *March 2013*, 4–26 March 2013; *November 2013*, 4–30 November 2014; *March–April 2014*, 15 March–12 April 2014, and the total number of samples collected at each site.

Elevational band – site	Latitude (°S)	Longitude (°E)	Elevation (m asl)	March 2013	November 2013	March–April 2014	No. samples
200 – 1	21.0766	148.6878	194		X	X	2
200 – 2	21.0746	148.6849	178		X	X	2
200 – 3	21.0764	148.6793	212		X	X	2
200 – 4	21.0673	148.6351	251		X	X	2
400 – 1	21.0619	148.6358	373	X	X	X	3
400 – 2	21.0611	148.6348	397	X			1
400 – 3	21.0614	148.6369	371	X			1

Elevational band – site	Latitude (°S)	Longitude (°E)	Elevation (m asl)	March 2013	November 2013	March–April 2014	No. samples
400 – 4	21.0605	148.6376	390	X	X	X	3
400 – 5	21.0597	148.6370	431	X			1
400 – 6	21.0702	148.6865	374		X	X	2
400 – 7	21.0655	148.6830	432		X	X	2
600 – 1	21.0564	148.6353	575	X	X	X	3
600 – 2	21.0556	148.6352	591	X			1
600 – 3	21.0556	148.6364	595	X			1
600 – 4	21.0548	148.6355	615	X	X	X	3
600 – 5	21.0539	148.6366	657	X			1
600 – 6	21.0634	148.6792	580		X	X	2
600 – 7	21.0623	148.6772	628		X	X	2
800 – 1	21.1447	148.4981	778	X			1
800 – 2	21.1431	148.4970	772	X	X	X	3
800 – 3	21.1429	148.4947	775	X			1
800 – 4	21.1413	148.4939	769	X	X	X	3
800 – 5	21.1491	148.5025	776	X			1
800 – 6	21.1218	148.5033	854		X	X	2
800 – 7	21.1438	148.4891	858		X	X	2
1000 – 1	21.0589	1485818	1022	X	X	X	3
1000 – 2	21.0512	148.5806	998	X	X	X	3
1000 – 3	21.0358	148.5970	1002	X	X	X	3
1000 – 4	21.0350	148.6003	988	X	X	X	3
1000 – 5	21.0302	148.6035	971	X			1
1200 – 1	21.0169	148.5980	1234		X	X	2
1200 – 2	21.0151	148.6084	1172		X	X	2
1200 – 3	21.0262	148.6274	1169		X	X	2
1200 – 4	21.0256	148.6384	1232		X	X	2

Ant Sampling

At each site a central 20 m × 20 m quadrat was established, where most ant sampling was conducted.

The same sampling methodology was employed at each site over the three survey periods: March 2013, November 2014, and March–April 2014. Five methods were used to sample the ant fauna of each site: leaf litter extraction ('litter extracts'), spraying tree trunks with insecticide ('bark sprays'), Malaise traps, pitfall traps, and timed hand collecting during the day ('day hand'). Samples were collected within the central quadrat of each site except for day hand samples. Each litter extract (two per site per survey) was derived from 1 m^2 of sifted leaf litter processed in a Tullgren funnel for 24–36 hours (wetter litter was extracted for longer). For each bark spray sample (two per site per survey), the trunks of five large trees (>30 cm dbh) were sprayed using hand-held cans of Mortein Fast Knockdown® pyrethroid insecticide. Falling insects were collected on a rectangular sheet of rip-stop at the base of each tree, and after around 15 minutes the catches on the five sheets were transferred to an

ethanol-filled vial using a suspended fabric funnel. A single day hand sample was collected per site per survey, where CJB searched for foraging ant workers and ant nests for 60 minutes within a 40–50 m radius of the centre of the quadrat, between 0905 and 1650 hours. Not all observed ants were collected; rather, the aim was to maximise the number of species collected. Ten pitfall traps were established at each site and operated for ten days. Traps were 42 mm internal diameter, 120 ml plastic vials half filled with 95% ethanol, with a square, black plastic rain cover suspended 3–4 cm above the opening. The ten traps were arranged in a line spanning one of the diagonals of the site quadrat (traps 2.5–3.0 m apart). A single Townes-type Malaise trap was operated for 10 days at each site. More detailed descriptions of the sampling methods can be found in Burwell & Nakamura (2016).

Sorting and Identification

Worker ants were extracted from all samples and identified to genus and morphospecies or described species (collectively referred to as 'species' hereafter) by CJB. The only exception was in the genus *Solenopsis*, represented by minute litter-inhabiting thief ants, where we did not attempt to divide our specimens into morphospecies. Identification of species of *Solenopsis* is notoriously difficult, and the presence of cryptic species is possible as has been demonstrated along a 2000 m elevational gradient in the Ecuadorian Andes (Delsinne *et al*., 2012). A voucher collection of pinned representatives of all species is deposited in the Queensland Museum. Subfamily, generic and species-level classification largely follows that adopted by the Australian Faunal Directory (https://biodiversity.org.au/afd/taxa/FORMICIDAE/checklist, last accessed 28 October 2018), except for relatively recent taxonomic developments. *Colobopsis* is treated as a valid genus distinct from *Camponotus* (Ward *et al*., 2016), and *Machomyrma* is treated as a synonym of *Pheidole* (Ward *et al*., 2015). For many genera, species collected along the Eungella gradient were compared and matched with species collected along two other rainforest gradients of elevation in Queensland, one at Lamington National Park (28.1°S) in subtropical south-eastern Queensland and one in tropical northern Queensland at Mt Lewis (16.3°S) in the Carbine Uplands subregion of the Wet Tropics. At the Mt Lewis gradient, four sites at each of five elevational bands (400, 600, 800, 1000 and 1200 m asl) were sampled once in March 2012 using the same sampling protocol used at Eungella (see Burwell & Nakamura, 2016 for more details). At the Lamington gradient, four sites at each of five elevational bands (300, 500, 700, 900 and 1100 m asl) were sampled three times in October 2006, March 2007 and January 2008) using the same methods used at Eungella. We place more emphasis on comparisons between the Eungella and Lamington gradients as the sampling intensity at each was relatively similar. We also comment on the known extent of the distribution of particular ant species. This information is drawn either from the taxonomic literature or through examination of distribution records accessed using online resources: *Atlas of Living Australia* (ALA, https://www.ala.org.au/) and *Antmaps* (http://antmaps.org/; Janicki *et al*., 2016).

Data Analysis

In this study, a sample consisted of specimens collected from a given site at a given survey period. The total number of samples in each elevational band therefore varied between eight and thirteen (Table 1). Data from all five collecting methods were pooled for each sample and species abundances transformed to incidences (presence/absence). We first summarised the elevational distributions of species along the Eungella gradient. For each elevational band we summed the number of samples from which a species was recorded. We then expressed that value as a percentage of the total number of samples for that particular elevational band (Table 1). In addition, we collated the total numbers of species collected within each elevational band.

We visualised patterns of ant species composition among sites by generating a non-metric multidimensional scaling (NMDS) ordination using PRIMER 6 software. Each point on the NMDS ordination corresponded to an individual sample (i.e. 8 samples for 200 and 1200 m asl bands, and 13 samples for 400, 600, 800 and 1000 m asl bands). The ordination was generated based on a Sørensen similarity matrix and 100 random restarts.

RESULTS AND DISCUSSION

In total, we recorded at least 142 ant species across our survey sites spanning the entire gradient of elevation (Table 2). We also observed green tree ants, *Oecophylla smaragdina*, in the riparian rainforest along Owens Creek, although this species was not collected from any of our survey sites, bringing the total ant fauna to at least 143 species. These species represented 62 genera from all 12 subfamilies currently recognised and recorded from Australia (Table 3). Some of the

mid-elevation sites consisted of rainforest understorey with a eucalypt canopy. This may have resulted in the collection of a small number of ant species typically found in more open habitats; *viz*. the species of *Cardiocondyla*, *Opisthopsis* and *Polyrhachis ornata* and *Polyrhachis erato* (see Table 2).

With the caveat of unequal sampling effort across the elevational gradient (fewer surveys and unique sites at 200 and 1200 m asl, and fewer sites at 1000 m asl), species richness was highest at mid-elevations, 89 species at 600 m asl, and declined as elevation both increased and decreased (Figure 1). The lowest number of species, 33, was recorded at the highest elevation, 1200 m asl, followed by 46 species at 1000 m asl (Figure 1). In terms of species composition, we found progressive turnover in ant assemblages with increasing elevation (Figure 2). There appeared, however, to be two different gradients of turnover, one in the lowlands from 200 to 600 m asl and another in the highlands from 800 to 1200 m asl (Figure 2).

TABLE 2. List of ant species collected during elevational surveys of rainforest in the Eungella region. Three surveys were conducted: March 2013 (five sites at each of four bands of elevation at approximately 400, 600, 800 and 1000 m above sea level (asl); and November 2013 and March–April 2014 (four sites at each of six bands of elevation at approximately 200, 400, 600, 800, 1000 and 1200 m asl). Shading indicates the bands of elevation where species were recorded; density of shading reflects the percentage of the total number of samples that a species was recorded. Shading reflects 10% increments from the palest (>0–10%) to the darkest (>90–100%), viz.:

>0–10	>10–20	>20–30	>30–40	>40–50	>50–60	>60–70	>70–80	>80–90	>90–100

Total possible samples from which a species could be recorded at each elevation were 13 for 400, 600, 800 and 1000 m bands, and 8 for the 200 and 1200 m bands (see Table 1).

SUBFAMILY ***Species***	**Elevational band (metres asl)**					
	200	**400**	**600**	**800**	**1000**	**1200**
AMBLYOPONINAE						
Amblyopone australis						
Amblyopone hackeri						
Onychomyrmex QM.1						
Onychomyrmex QM.2						
Onychomyrmex QM.3						
Onychomyrmex sp. A						
Prionopelta robynmae						
DOLICHODERINAE						
Anonychomyrma QM.3						
Anonychomyrma QM.4						
Anonychomyrma QM.5						
Anonychomyrma QM.8						
Anonychomyrma QM.9						
Iridomyrmex calvus						
Leptomyrmex mjobergi						
Leptomyrmex rufipes						
Ochetellus sp. C						
Tapinoma QM.2						

SUBFAMILY ***Species***	**Elevational band (metres asl)**					
	200	**400**	**600**	**800**	**1000**	**1200**
Tapinoma QM.3						
Tapinoma QM.4						
Technomyrmex jocosus						
Turneria bidentata						
DORYLINAE						
Lioponera sp. A (*turneri* group)						
Zasphinctus ?duchaussoyi						
Zasphinctus ?steinheili						
Zasphinctus turneri						
ECTATOMMINAE						
Rhytidoponera chalybaea						
Rhytidoponera impressa						
Rhytidoponera QM.12						
Rhytidoponera QM.14						
Rhytidoponera victoriae						
FORMICIDAE						
Acropyga acutiventris						
Acropyga pallida						
Camponotus dorycus confusus						
Camponotus sp. A						
Camponotus sp. B						
Camponotus sp. C						
Colobopsis sp. D						
Colobopsis sp. F						
Colobopsis vitrea						
Echinopla turneri						
Myrmecorhynchus emeryi						
Notoncus sp. nov.						
Notostigma carazzii						
Nylanderia QM.1						
Oecophylla smaragdina	0					
Opisthopsis pictus						
Paraparatrechina QM.4						
Paraparatrechina QM.9						

SUBFAMILY *Species*	**Elevational band (metres asl)**					
	200	**400**	**600**	**800**	**1000**	**1200**
Polyrhachis (Campomyrma) sp. nov.						
Polyrhachis (Campomyrma) maculata						
Polyrhachis (Cyrtomyrma) mackayi						
Polyrhachis (Cyrtomyrma) pilosa						
Polyrhachis (Hedomyrma) sp. nov						
Polyrhachis (Hedomyrma) argentosa						
Polyrhachis (Hedomyrma) clio						
Polyrhachis (Hedomyrma) erato						
Polyrhachis (*Hedomyrma*) *ornatus*						
Polyrhachis (*Hedomyrma*) *rufifemur*						
Prolasius formicoides						
Prolasius convexus						
Pseudonotoncus hirsutus						
Stigmacros major						
HETEROPONERINAE						
Heteroponera crozieri						
Heteroponera sp. A (*imbellis*-grp)						
LEPTANILLINAE						
Leptanilla swani						
MYRMECIINAE						
Myrmecia eungellensis						
Myrmecia nigrocincta						
MYRMICINAE						
Aphaenogaster pythia						
Calyptomyrmex fragarus						
Cardiocondyla sp. A						
Carebara sp. A						
Carebara sp. B						
Carebara sp. C						
Colobostrum australis						
Colobostruma leae						
Colobostruma sisypha						
Crematogaster sp. A						
Crematogaster sp. B						

SUBFAMILY ***Species***	**Elevational band (metres asl)**					
	200	**400**	**600**	**800**	**1000**	**1200**
Crematogaster sp. C						
Crematogaster sp. D						
Crematogaster sp. E						
Eurhopalothrix australis						
Lordomyrma sp. A						
Mayriella abstinens						
Mayriella overbecki						
Mayriella spinosior						
Meranoplus hirsutus						
Monomorium kiliani						
Monomorium 'leae'						
Monomorium near *intrudens*						
Monomorium nigriceps						
Monomorium sp. B						
Monomorium sp. D						
Monomorium tambourinense						
Myrmecina difficulta						
Myrmecina inaequala						
Orectognathus mjobergi						
Orectognathus parvispinus						
Orectognathus near *coccinatus*						
Orectognathus versicolor						
Pheidole dispar						
Pheidole sp. A						
Pheidole sp. B						
Pheidole sp. C						
Pheidole sp. D						
Pheidole sp. E						
Pheidole sp. F						
Podomyrma sp. A						
Podomyrma sp. B (*novemdentata*-grp)						
Podomyrma sp. C (*turneri*-grp)						
Podomyrma basalis						
Podomyrma sp. E (*novemdentata*-grp)						

SUBFAMILY ***Species***	**Elevational band (metres asl)**					
	200	**400**	**600**	**800**	**1000**	**1200**
Podomyrma ?delbrueckii						
Podomyrma sp. G						
Pristomyrmex foveolatus						
Rhopalothrix orbis						
Solenopsis						
Strumigenys deuteras						
Strumigenys emdeni						
Strumigenys guttulata						
Strumigenys near *perplexa*						
Strumigenys varanga						
Strumigenys zygon						
Syllophopsis sp. A						
PONERINAE						
Anochetus graeffei						
Cryptopone rotundiceps						
Hypoponera sp. A						
Hypoponera sp. B						
Hypoponera sp. C						
Hypoponera sp. E						
Leptogenys bidentata						
Leptogenys nr *mjobergi*						
Leptogenys turneri						
Mesoponera australis						
Platythyrea parallela						
Ponera leae						
Pseudoneoponera sp. A						
Pseudoneoponera sp. B						
PROCERATIINAE						
Discothyrea sp. A						
Discothyrea sp. B						
Discothyrea sp. C						
Proceratium australe						
PSEUDOMYRMECINAE						
Tetraponera punctulata						

FIGURE 1. Overall number of ant species collected from each band of elevation at Eungella (bars) and at Lamington (points), showing broad patterns of species richness across elevation. Richness values between transects are not directly comparable due to differing sampling intensity (see Burwell & Nakamura, 2011, for details of sampling protocol at Lamington). At Eungella, sampling intensity varied among elevational bands both in terms of the number of unique sites (four at 200 m and 1200 m, five at 1000 m, and seven at 400, 600 and 800 m) and the number of samples (eight at 200 and 1200 m, and 13 at 400, 600, 800 and 1000 m).

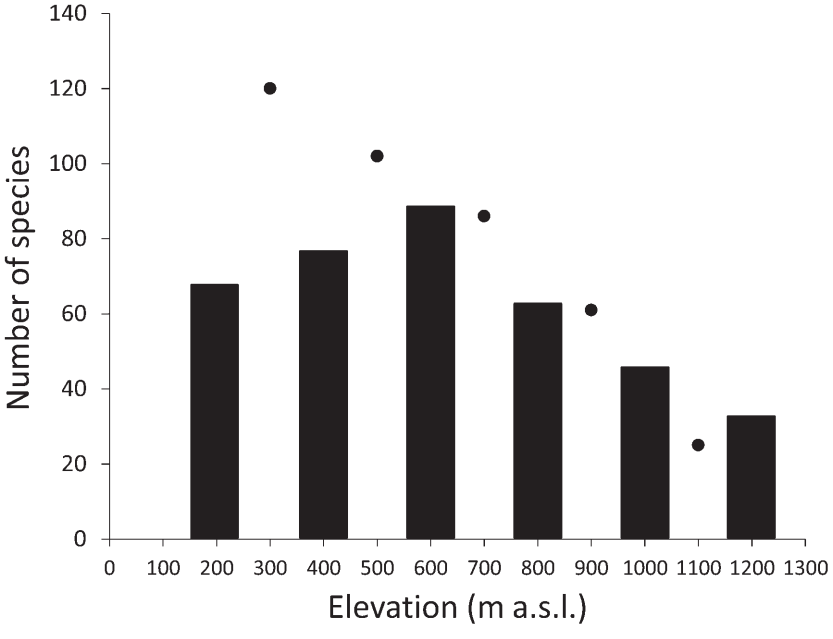

FIGURE 2. NMDS ordination of ant species assemblages from samples collected along a gradient of elevation in the Eungella region. Ordination based on incidence (presence/absence) of species from pooled data from five different sampling methods. Solid oval encloses low-elevation samples from 200 to 600 m asl, and dashed oval encloses high-elevation samples from 800 to 1200 m asl.

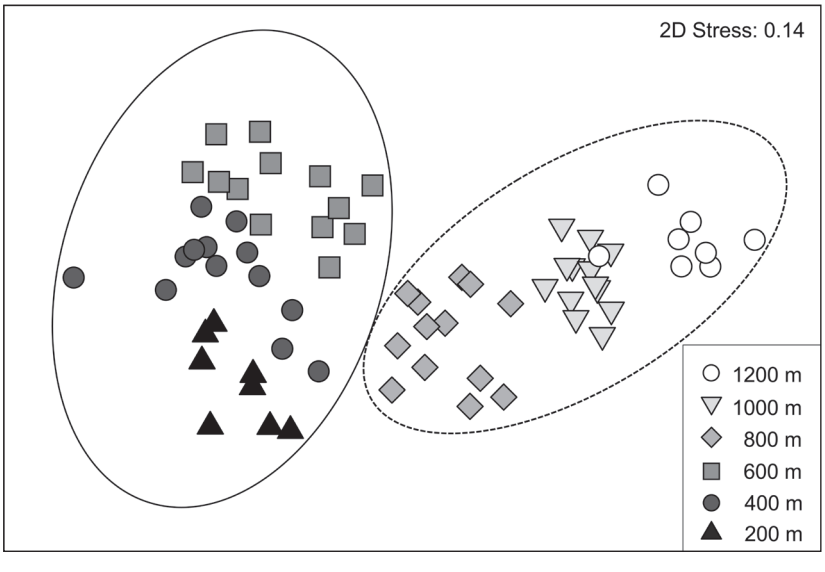

TABLE 3. Subfamily and generic distribution of 142 ant species and the genus *Solenopsis*, recorded from the entire Eungella elevational gradient. Genera marked with an asterisk contained at least one species considered to be characteristic of more open forest habitats. NA – not applicable, as specimens of *Solenopsis* were not sorted to morphospecies.

Genus	# spp.
AMBLYOPONINAE	
Amblyopone	2
Onychomyrmex	4
Prionopelta	1
DOLICHODERINAE	
Anonychomyrma	5
Iridomyrmex	1
Leptomyrmex	2
*Ochetellus**	1
Tapinoma	3
Technomyrmex	1
Turneria	1
DORYLINAE	
Lioponera	1
Zasphinctus	3
ECTATOMMINAE	
Rhytidoponera	5
FORMICINAE	
Acropyga	2
Camponotus	4
Colobopsis	3
Echinopla	1
Myrmecorhynchus	1
Notoncus	1
Notostigma	1
Nylanderia	1

Genus	# spp.
FORMICINAE (*cont.*)	
Oecophylla	1
*Opisthopsis**	1
Paraparatrechina	2
*Polyrhachis**	10
Prolasius	2
Pseudonotoncus	1
Stigmacros	1
HETEROPONERINAE	
Heteroponera	2
LEPTANILLINAE	
Leptanilla	1
MYRMECIINAE	
Myrmecia	2
MYRMICINAE	
Aphaenogaster	1
Calyptomyrmex	1
*Cardiocondyla**	1
Carebara	3
Colobostruma	3
Crematogaster	5
Eurhopalothrix	1
Lordomyrma	1
Mayriella	3
Meranoplus	1
Monomorium	7

Genus	# spp.
MYRMICINAE (*cont.*)	
Myrmecina	2
Orectognathus	4
Pheidole	7
Podomyrma	7
Pristomyrmex	1
Rhopalothrix	1
Solenopsis	NA
Strumigenys	6
Syllophopsis	1
PONERINAE	
Anochetus	1
Cryptopone	1
Hypoponera	4
Leptogenys	3
Mesoponera	1
Platythyrea	1
Ponera	1
Pseudoneoponera	2
PROCERATIINAE	
Discothyrea	3
Proceratium	1
PSEUDOMYRMECINAE	
Tetraponera	1
TOTAL GENERA	62
TOTAL SPECIES	143

Below we provide an overview of the fauna of each subfamily, highlighting records of interest. We also compare our data with the species recorded along elevational gradients in subtropical rainforest at Lamington National Park (300 to 1100 m asl) in south-eastern Queensland, and tropical rainforest at Mt Lewis (200 to 1200 m asl) in the Wet Tropics bioregion in northern Queensland.

Subfamily Amblyoponinae (3 genera, 7 species)

We recorded two species of *Amblyopone*. *Amblyopone australis* occurred across the entire gradient, becoming more frequently collected as elevation increased; it was recorded from all 1200 m asl sites each time they were surveyed. At Lamington in south-eastern Queensland, the same pattern was observed with *A. australis* occurring across the entire gradient from 300 to 1100 m asl, increasing in frequency with increasing elevation. In contrast, at Eungella *Amblyopone hackeri* was collected infrequently and only from sites at 1000 m asl. This species was originally described from Lamington National Park and is known from south-eastern Queensland and eastern New South Wales as far south as Sydney. There is a previous record of *A. hackeri* from Eungella National Park (Australian National Insect Collection sourced via the ALA). The Eungella population is highly disjunct and appears restricted to the high-elevation subtropical forests.

The litter-inhabiting *Prionopelta robynmae* was recorded infrequently from sites at only 600 m asl. This is a widely distributed species of *Prionopelta* occurring from Papua New Guinea and from eastern coastal Australia as far south as Victoria, with records from the Top End of the Northern Territory (Shattuck, 2008). At Lamington, *P. robynmae* occurred from 300–900 m asl.

Four species of *Onychomyrmex* were infrequently collected from 400 to 1200 m asl. As there has been no recent taxonomic revision of *Onychomyrmex*, none were assigned to described species. *Onychomyrmex*

is confined to Australia, with most species distributed along the east coast from Cape York Peninsula to south-eastern Queensland. A single species, *O. glauerti*, recently transferred to *Onychomyrmex* by Ward & Fisher (2016), is also known from south-western Western Australia. Along the east coast, *Onychomyrmex* is essentially tropical, with a single undescribed species known from subtropical, south-eastern Queensland (Lamington National Park, 500 and 900 m asl, CJB unpublished data). We also recorded the south-eastern Queensland species, *Onychomyrmex* QM.1, from Eungella at a single site at 1000 m asl in March 2014. Two of the remaining *Onychomyrmex* species from Eungella were not represented from our Lamington and Mt Lewis gradients, but a very small, pale species, *Onychomyrmex* sp. A, collected once from 200 m asl at Owens Creek, closely resembles a species collected once from Mt Lewis at 400 m asl.

Subfamily Dolichoderinae (7 genera, 14 species)

Dolichoderines were relatively poorly represented in our surveys, with only fourteen species from seven genera: *Anonychomyrma* (5 species), *Tapinoma* (3 spp.), *Leptomyrmex* (2 spp.), and single species each of *Iridomyrmex*, *Ochetellus*, *Technomyrmex* and *Turneria*.

Two of the species of *Anonychomyrma* are of note because they co-occurred on either our Mt Lewis or Lamington gradients. *Anonychomyrma* QM.4 is a relatively large and densely pilose species that may be *Anonychomyrma gilberti*. At Eungella this species was recorded from 200 to 1000 m asl. At lower elevations it was particularly abundant and ubiquitous: it was recorded from all surveys of all sites from 200 to 600 m asl. With increasing elevation it became more spatially and temporally patchy, recorded from 77% and 23% of site surveys at 800 m asl and 1000 m asl, respectively, and was not collected at any 1200 m asl sites. At Mt Lewis in the Wet Tropics this species occurred from 400 to 1200 m asl, but oddly was not recorded from sites at 1000 m asl. This is a largely arboreal species, and differences in the structure of the forest at the upper elevations at Mt Lewis – the canopy at 1000 m was much higher than at 1200 m asl – may explain why we did not sample the species at ground level.

The smaller *Anonychomyrma* QM.3 inhabited higher elevations at 800, 1000 and 1200 m asl, where it was recorded from 46% of surveyed sites at 800 m and all sites at 1000 m and 1200 m. In contrast, at Lamington *Anonychomyrma* QM.3 occurred at much lower elevations and was recorded from all survey sites between 300 and 900 m asl, and half the sites at 1100 m asl. The degree of the downslope extension of its range in the subtropics seems unlikely to be due only to the influence of the higher latitude. It may be that the populations of *Anonychomyrma* QM.3 at Eungella and Lamington are not conspecific but rather different species with differing thermal tolerances. Alternatively, perhaps the ubiquity of *Anonychomyrma* QM.4 at lower elevations on the Eungella gradient displaces *Anonychomyrma* QM.3 upslope.

Three species of *Tapinoma* were recorded from the Eungella gradient, all of which also occurred at Lamington, and one, *Tapinoma* QM.2, that also occurred at Mt Lewis. This species was only recorded from a single site at 600 m asl at Mt Lewis, whereas it occurred over most of the gradient at Eungella and Lamington: 200–1000 m asl and 300–1100 m asl, respectively.

The single species of *Technomyrmex* collected at Eungella, *T. jocosus*, was recorded from the entire elevational gradient (200–1200 m asl). It also occurred at Lamington, but only from 300–700 m asl. *Technomyrmex jocosus* is widely distributed in Australia, occurring along the east coast from the Wet Tropics, Queensland to Tasmania, Victoria and southern South Australia, and extending west to south-western Western Australia (Bolton, 2007). Two species of 'spider ant' were recorded in our surveys, *Leptomyrmex rufipes* (400–800 m asl) and *Leptomyrmex mjobergi* (200–600 m asl), both of which have been previously recorded from the Eungella region (Lucky & Ward, 2010). *Leptomyrmex mjobergi* occurs along the east coast from the northern Wet Tropics south to the Queensland-New South Wales border (Lucky & Ward, 2010) but was not collected at either our Mt Lewis or Lamington gradients. *Leptomyrmex rufipes* has a similar distribution but extends to the base of Cape York Peninsula in the north (Lucky & Ward, 2010). Similarly, *L. rufipes* was not recorded from the Mt Lewis gradient, and only a single specimen was collected from a 200 m asl plot at Lamington.

Turneria bidentata is an arboreal, lignicolous species which, like many formicines with comparable nesting habits, was recorded from lower elevations (200–600 m asl) at Eungella. In Australia, *T. bidentata* is known from the Top End of the Northern Territory and along the east coast from Cape York south to about Taree in northern New South Wales (Shattuck, 1990; records sourced from the ALA). A single species of

Iridomyrmex, *I. calvus*, was recorded from our surveys, from single sites at each of 400 and 600 m asl. *Iridomyrmex calvus* is known from the southern Australian mainland, Tasmania, Lord Howe Island, Norfolk Island and New Caledonia (Heterick & Shattuck, 2011). Specimens of *I. calvus* from Australia were originally described as *I. notialis* (Shattuck, 1993). Our collections represent the northernmost Australian records of the species.

Subfamily Dorylinae (2 genera, 4 species)

Several collections of *Lioponera*, often previously referred to as *Cerapachys* (e.g. Shattuck, 1999), were made across the full elevational gradient (200 to 1200 m asl). Specimens varied somewhat in size, the shape of the postpetiole and the form of the frontal carinae. This variation, however, is difficult to interpret, and we have taken a conservative approach and consider them all conspecific at present. They belong to the *turneri* species group of Brown (1975) which comprises mostly small, predominantly black species inhabiting forests in eastern and south-western Australia, New Guinea and New Caledonia.

Three distinct species of *Zasphinctus*, often previously referred to as *Sphinctomyrmex* (e.g. Shattuck, 1999), were represented among our collections. The large, dark *Zasphinctus turneri* was collected once from pitfall traps at 200 m asl. This species has relatively large eyes and twelve-segmented antennae, and has been recorded from the Wet Tropics south to west of Bundaberg, Queensland. The two other *Zasphinctus* belong to Brown's (1975) *steinheili* species group, consisting of species with 11-segmented antennae and eyeless workers from Australia, New Guinea and New Caledonia. One is probably *Z. steinheili* itself, originally described from specimens from Mackay, and was collected from sites at 600–1200 m asl. The second, which may be *Z. duchaussoyi*, was represented by a single collection of very small, pale-coloured workers from a site at 600 m asl.

Subfamily Ectatomminae (1 genus, 5 species)

Five species of *Rhytidoponera* were recorded in our surveys, three of which have been assigned to described species. Two belong to the *impressa*-group of species revised by Ward (1980): *R. chalybaea* and *R. impressa*. *Rhytidoponera chalybaea* was confined to sites at 1200 and 1000 m asl, and was replaced by *R. impressa* at 800 m asl, the only elevation from which the latter species was recorded. Both showed high site and temporal fidelity, particularly *R. chalybaea*, occurring at most sites and most survey occasions within their elevational ranges. *Rhytidoponera chalybaea* is a common ant of subtropical rainforest in southern Queensland and northern New South Wales (Ward, 1980). At our Lamington gradient in south-eastern Queensland, it was common and confined to sites at 300, 500 and 700 m asl, occurring at lower elevations at the higher latitude. Given that *R. chalybaea* was common as low as 300 m asl at Lamington, it might be expected to occur at lower elevations than those recorded at Eungella. However, species interactions may explain this anomaly, given that it was replaced by the closely related *R. impressa* at 800 m asl at Eungella.

In contrast, the elevational range of *Rhytidoponera victoriae*, a member of the *metallica*-group of species, did not differ substantially between the Eungella and Lamington gradients. It was recorded from the majority of sites at 200, 400 and 600 m asl at Eungella, and at Lamington it was recorded from 300 and 700 m asl. At Mt Lewis, however, the elevational range of *R. victoriae* did appear to shift upslope, occurring from 600 to 1000 m asl. The remaining *Rhytidoponera* species from Eungella, *Rhytidoponera* QM.12 (200–600 m asl) and *Rhytidoponera* QM.14 (400–800 m asl), were not recorded from either our Lamington or Mt Lewis gradients.

Subfamily Formicinae (15 genera, 32 species)

This was the second most diverse subfamily represented in our Eungella collections, both in terms of genera and species. The most speciose genera were *Polyrhachis* (10 species), *Camponotus* (4 spp.) and *Colobopsis* (3 spp.), with all other genera represented by one or two species.

Two described species of *Acropyga* were recorded: *Acropyga acutiventris* from two adjacent sites at 600 m asl, and *Acropyga pallida* from a single collection from a site at 800 m asl. Species of *Acropyga* are subterranean ants that live in obligate symbiotic associations with root mealybugs (Pseudococcidae) (Blaimer *et al*., 2016), although one Australian species has been found associated with a species of Orthezidae (LaPolla *et al*., 2008). *Acropyga acutiventris* is a tropical species that is widespread in the Oriental, Indo-Australian and Australasian regions (LaPolla, 2004). In Australia, it has been recorded from the Top End of the Northern Territory, and in Queensland from Cape York Peninsula south to Eungella (Taylor, 1992; LaPolla, 2004). *Acropyga pallida* occurs from Australia north to the Philippines and west to Borneo

(La Polla, 2004). It is widespread in Australia, with records from northern Western Australia, the Top End of the Northern Territory, and along the east coast from Cape York Peninsula south to Victoria (Lapolla, 2004). Our collection appears to be the first record of the species from the Eungella region. The third Australian species in the genus, *Acropyga myops*, has also been recorded from the Eungella region, but from dry sclerophyll forest (LaPolla, 2004).

A single species of the endemic Australian genus *Myrmecorhynchus*, *M. emeryi*, was recorded from our surveys. *Myrmecorhynchus* is confined to southern and eastern Australia, with three described species with largely arboreal workers (Shattuck, 2015). *Myrmecorhynchus emeryi* is the most widespread, occurring across the southern mainland from south-western Western Australia to southern South Australia, Victoria, eastern New South Wales and south-eastern Queensland (Shattuck, 2015). In addition to our collections, Shattuck (2015) listed specimens from Eungella, which is the northernmost extent of the range of the species. At Eungella, *Myrmecorhynchus emeryi* occurred at sites from 600 to 1200 m asl, and became increasingly common as elevation increased: it was ubiquitous at sites at 1000 and 1200 m asl. At subtropical Lamington, the elevational range of *M. emeryi* was slightly lower, where it was ubiquitous at sites from 500 to 900 m asl but was not recorded from any sites at 1100 m asl.

Two species of *Prolasius* were recorded from the Eungella gradient which have different distribution patterns. One, *Prolasius formicoides*, originally described from Mackay, occurred from as low as 400 m asl to the highest elevations at 1200 m asl. *Prolasius formicoides* is very closely allied, and may well by synonymous with *Prolasius mjoebergella* (Taylor, 1992) originally described from Malanda in the Wet Tropics. *P. mjoebergella* is widespread in the Wet Tropics, and on our Mt Lewis transect occurred from 800 and 1200 m asl, suggesting an upslope shift of its elevational range at lower latitudes if it is indeed synonymous with *P. formicoides*. The other species recorded from Eungella, *Prolasius convexus*, has a more southerly distribution and was originally described from Dorrigo in northern New South Wales. This arboreal species occurred at our south-eastern Lamington gradient from 500 to 900 m asl (Burwell & Nakamura, 2011), whereas at Eungella it was recorded only from 1000 m asl from all five survey sites.

Notostigma carazzii, one of the two species of this Australian endemic genus, is widespread throughout the Wet Tropics bioregion, occurring as far south as Mt Elliot south of Townsville (Taylor, 1992; additional records sourced via the ALA). This species is also known from the Eungella region (Taylor, 1992), the southernmost extent of its range, where we recorded it from sites at 600 to 800 m asl.

Formicine species that nest arboreally were more diverse at lower elevations, 200–600 m asl, of the Eungella gradient, and included both lignicolous and weaving species. Weavers included two species of the subgenus *Cyrtomyrma* of the genus *Polyrhachis* (*Polyrhachis pilosa* and *Polyrhachis mackayi*) and the green tree ant *Oecophylla smaragdina*. Aboreal, lignicolous species, that is, those nesting in hollows in twigs and branches, included *Echinopla turneri*, several species of *Polyrhachis* in the subgenera *Campomyrma* and *Hedomyrma*, and a number of *Colobopsis* species. It should be noted that *Campomyrma* as currently applied appears polyphyletic, with the Australian species forming a clade distinct from the 'true' *Campomyrma* species from Southeast Asia (Mezger & Moreau, 2016). Many of these arboreal nesters from Eungella are largely tropical species. In Australia, *Colobopsis vitrea*, for example, occurs in the Top End of the Northern Territory and in north-eastern Queensland from Cape York south to Mackay (McArthur & Shattuck, 2001). Records of the species from south-eastern Queensland (Mt Coot-tha, Brisbane, Goodna) listed by McArthur & Shattuck (2001) are almost certainly erroneous. Similarly, *Oecophylla smaragdina* is widespread in northern Australia, and extends throughout the tropical east coast of Queensland, extending as far south as Rockhampton and Gladstone in the subtropics (Wetterer, 2017). *Polyrhachis (Hedomyrma) argentosa* shows a similar distribution pattern, occurring from south of Cooktown to the Rundle Range near Gladstone (Kohout, 2000). *Echinopla turneri* has a more restricted distribution, occurring from the Paluma Range in the southern Wet Tropics bioregion south to Yeppoon (Kohout, 2000). Not all lignicolous formicines were confined to the lowlands, with a species of *Colobopsis* and *Polyrhachis (Campomyrma)* collected from sites at 1000 and 1200 m asl.

We recorded a single species of the largely southern Australian genus *Stigmacros*, *Stigmacros major*, along the Eungella gradient. Originally described from Lamington National Park, *S. major* was also collected from our Lamington gradient (Burwell & Nakamura, 2011). Despite the latitudinal difference in the location of the gradients, *S. major* occurred at similar elevations at both Lamington (300–700 m asl) and Eungella (400–600 m asl).

Subfamily Heteroponerinae (1 genus, 2 species)

What we tentatively identified as a single species of *Heteroponera* in the *H. imbellis* species group (*sensu* Taylor, 2011) was recorded from across the entire Eungella elevational gradient. This species-group is known from Iron Range on Cape York Peninsula and from around Cooktown, Queensland, south to southern New South Wales and Victoria, extending west to southern South Australia and south-western Western Australia. Taylor (2011) estimated the group to be represented by six species in collections. The second species of *Heteroponera* recorded in our surveys, *H. crozieri*, is a member of the *leae* species group. This species has previously been recorded from Eungella and occurs from the Clarke Range south to south-eastern Queensland and north-eastern New South Wales (Taylor, 2011). No species of the *relicta* species group, which is confined to the Wet Tropics bioregion (Taylor, 2015), were collected at Eungella.

Subfamily Leptanillinae (1 genus, 1 species)

The subfamily Leptanillinae is represented in Australia by the single widespread species *Leptanilla swani* which also occurs in New Guinea. Although widespread, most records of the species are of alate males, and the subterranean workers are very rarely collected. Two collections of *Leptanilla* workers and associated larvae were made during the Eungella survey, one from 600 m asl and a second from 800 m asl, and are assumed to be *L. swani* based on Baroni Urbani's worker-based key and comparison with images of the types of *L. swani* available on ANTWEB.

Subfamily Myrmeciinae (1 genus, 2 species)

Two species of *Myrmecia* were recorded during our surveys. *Myrmecia nigrocincta* was primarily a lowland species, recorded from sites at 200 and 400 m asl with a single collection at 600 m asl. This is a widespread species occurring in eastern Australia from the Wet Tropics in Queensland south to Victoria (Ogata & Taylor, 1991). Specimens of a second large species of *Myrmecia* in the *gulosa* group (*sensu* Ogata & Taylor, 1991) were collected only at high-elevation sites at 1000 and 1200 m asl. Ogata & Taylor (1991) described two new, apparently endemic species of large *Myrmecia* from high elevations at Eungella, *M. eungellensis* and *M. fabricii*. The two species were very similar in appearance, and distinguished by the dimensions of the petiole and the form of the occipital carina and hairs on the body (Ogata & Taylor, 1991). Worker specimens from our collections were examined by R. W. Taylor who concluded that they were *M. eungellensis*. Our specimens show greater than expected variation in the dimensions of the petiole, but all have a complete occipital carina which distinguishes them from *M. fabricii* workers which have the carina interrupted medially. However, given the degree of variability in our specimens, there is a possibility that *M. eungellensis* and *M. fabricii* are synonymous (R. W. Taylor, *pers. comm.*).

Subfamily Myrmicinae (20 genera, 57 species)

By far the most diverse subfamily among our Eungella collections was the Myrmicinae with an estimated 57 species from 21 genera. The most speciose genera along the gradient were *Monomorium* (7 spp.), *Pheidole* (7 spp.), *Podomyrma* (7 spp.), *Strumigenys* (6 spp.), *Crematogaster* (5 spp.) and *Orectognathus* (4 spp.).

Calyptomyrmex is a rarely collected genus of cryptic, litter-inhabiting ants which, in Australia, is confined to tropical and subtropical Queensland and New South Wales (Shattuck, 2011). *Calyptomyrmex fragarus* was a lowland species, recorded from litter extracts from the majority of sites at 400 and 600 m asl, and a single site at 200 m asl. This species is known from the Bluewater and Paluma Ranges in the southern Wet Tropics, with a single previous record from Finch Hatton Gorge in the Eungella region (Shattuck, 2011). *Pristomyrmex foveolatus* was also only recorded from the lowlands (200–600 m asl), largely from litter extracts. This rainforest-inhabiting species has been recorded throughout the Wet Tropics and from a number of localities in the Central Queensland Coast: Mt Dryander, the Conway Range, and Finch Hatton Gorge in the Eungella region (Taylor, 1965; Wang, 2003). Other myrmicine genera with species largely collected from litter extracts included *Strumigenys* (6 spp.), *Carebara* (3 spp.), *Mayriella* (3 spp.), with *Lordomyrma*, *Eurhopalothrix* and *Rhopalothrix* all represented by single species.

Four species of the trap-jaw, dacetine genus *Orectognathus* were recorded along the Eungella gradient. *Orectognathus parvispinus* was originally described from Eungella (Taylor, 1977) and may be endemic to the region. The type series was collected from 780 m asl (Taylor, 1977), and we recorded it from sites at 800, 600 and 400 m asl. Two of the *Orectognathus* species also occurred at our Lamington gradient. *Orectognathus mjobergi* occurs along the eastern Australian coast from the Wet Tropics to central New South Wales

(Taylor, 1977). We recorded it only from 600 m asl at Eungella, whereas at Lamington it was collected only at 300 m asl. *Orectognathus versicolor* is known from coastal New South Wales north to south-eastern Queensland, with a disjunct population in the Eungella region (Taylor, 1977). At Lamington, *O. versicolor* occurred at most survey sites from 300 to 900 m asl, whereas at Eungella it was sampled only from higher elevations between 800 and 1200 m asl. The remaining *Orectognathus* was collected from single sites at both 600 and 800 m asl, and is an undescribed species close to *O. coccinatus*.

A number of species of *Monomorium* were collected along the gradient. Two species are of interest because they were also collected along our Lamington transect in south-eastern Queensland. One of these keys to *Monomorium kiliani* using Heterick's (2001) key to Australian species of *Monomorium*. According to Heterick (2001), *M. kiliani* is widespread in southern Australia, occurring from southern South Australia, Victoria, Tasmania and New South Wales. Records of *M. kiliani* from Western Australia are questionable (B. Heterick, *pers. comm.*). At Eungella, *M. kiliani* was collected only once in pitfalls at a 1200 m asl site in March 2014; this collection represents a substantial northern extension of the known range of the species. At our Lamington gradient, this species was recorded from sites at 500, 700 and 1200 m asl. At Lamington, it appeared to be more active in cooler seasons. In surveys conducted in the austral summer, early autumn and mid-spring (January, February, March and October), *M. kiliani* was detected in low numbers only at the highest elevations of the Lamington gradient (1100 m asl). In mid-winter, however, the abundance of *M. kiliani* in litter extracts from 1100 m asl increased substantially, and it was detected in samples from one site at 700 m asl and three sites at 500 m asl. The second *Monomorium* species of interest keys to *M. leae* (which may well be a complex of species, B. Heterick, *pers. comm.*) using Heterick's (2001) key. It appeared to show an upslope shift in at least its lower elevational range at Eungella compared with Lamington, recorded from 300–1100 m asl at Lamington and 800–1200 m asl at Eungella.

Species of *Myrmecina* are small, cryptic ants most commonly collected from leaf litter extracts. The Australian fauna consists of 13 described species which are mostly found in north-eastern Australia (Shattuck, 2009). We recorded two species from the Eungella gradient: *Myrmecina difficulta* from 600–1200 m asl, and *Myrmecina inaequala* from 200–800 m asl.

Seven species of *Pheidole* were collected along the gradient but, in the absence of recent revisionary work on the Australian species, we have not attempted to assign them to described species nor matched them across the three elevational gradients. The exception was *Pheidole dispar*, which was previously included in the monotypic genus *Machomyrma* (see Shattuck, 1999) which has recently been synonymised with *Pheidole* (Ward *et al*., 2015). Within the Eungella transect, a number of *Pheidole* species appear good candidates for future monitoring of elevational range shifts due to warming temperatures. The genus includes species apparently confined to lower elevations (300–600 m asl – *Pheidole* sp. B and *Pheidole* sp. F) and another, *Pheidole* sp. E, confined to high elevations (1000–1200 m asl). These species also show quite high site and survey fidelity within their elevational ranges, increasing their suitability as indicator species.

The majority of Australian species within the myrmicine genera *Crematogaster* and *Podomyrma* are arboreal species generally nesting within hollows in twigs and branches, particularly in rainforest habitats. Both were well represented along the Eungella gradient, with the majority of species recorded from lower elevations between 200 and 600 m asl. However, this pattern should be treated with caution with regards to the *Podomyrma* species, given they were collected uncommonly and a number were recorded from higher elevations. The Australian fauna of both genera is in need of revision, and identification of the *Podomyrma* species was facilitated by an unpublished key to described species and species-groups supplied by R. W. Taylor.

Subfamily Ponerinae (8 genera, 14 species)

The subfamily Ponerinae was represented by at least 14 species in 8 genera. *Hypoponera* (at least four species), *Leptogenys* (3 spp.) and *Pseudoneoponera* (2 spp.) were the only genera with multiple species. *Anochetus*, *Cryptopone*, *Mesoponera*, *Ponera* and *Platythyrea* were all represented by single species.

Hypoponera is a taxonomically challenging genus, and we have only tentatively assigned specimens of the genus to morphospecies. As such, we did not identify any as described species, nor have we matched morphospecies across the Eungella, Lamington and Mt Lewis gradients. Three of the four Eungella morphospecies were largely ground-inhabiting, collected mainly in litter extracts, but one was usually collected under the rotten bark of fallen logs.

Among the species of *Leptogenys*, the small *Leptogenys bidentata*, originally described from Mackay, occurred along the entire length of the Eungella gradient (200–1200 m asl). *Leptogenys turneri*, a much larger species with a posterodorsal spine projecting from the petiolar node, was recorded from a single site at 200 m asl, and two sites at 1000 m asl. *Leptogenys turneri* was also originally described from Mackay and has been previously recorded from Eungella and the Paluma Range in the southern Wet Tropics bioregion (Taylor, 1988). According to Taylor (1988), the closely related *Leptogenys longensis*, which also possesses a spinose petiolar node, replaces *L. turneri* further north in the Wet Tropics from Kooboolloomba in the Atherton Uplands north to Cape Tribulation. The third *Leptogenys* species recorded in our surveys (800 and 1000 m asl) is close to *L. mjobergi* collected from our Lamington transect, but appears to be a distinct species. *Leptogenys excisa* is known from rainforests in the Eungella region (Taylor, 1988) but was not recorded on our surveys.

Two of the remaining ponerines, *Cryptopone rotundiceps* and *Mesoponera australis*, occurred across all three gradients. *Cryptopone rotundiceps* is usually found nesting in rotten, fallen logs, and its recorded elevational ranges across the three gradients were not consistent with the expectation of upslope range shifts associated with decreasing latitude. At Lamington, *C. rotundiceps* occurred from 500 to 1100 m asl (Burwell & Nakamura, 2011, as *Cryptopone* IBISCA.1), at Eungella only from 1000–1200 m asl, and at Mt Lewis (based on a single survey) from 600–1200 m asl. Similarly, the elevational ranges of the ground-nesting *Mesoponera australis* were difficult to interpret, as the ant only occurred at 300 m asl at Lamington (Burwell & Nakamura 2011, as *Pachycondyla australis*), and from 200 to 800 m asl at Eungella. At Mt Lewis it was collected only twice, once at 400 m asl and once from 1000 m asl.

Proceratiinae (2 genera, 4 species)

Three unidentified species of *Discothyea* and a single species of *Proceratium* were recorded from Eungella. The species of both genera are minute, litter-inhabiting ants, and the majority of our collections were from litter extracts. We also collected species of *Discothyrea* from our Lamington and Mt Lewis gradients but did not match them across the gradients as the specimens were unavailable. Single specimens of *Proceratium australe* were collected from each of our three Eungella surveys, one each from 200, 800 and 1000 m asl. *Proceratium australe* is a morphologically variable species occurring along the eastern Australian coast from the Wet Tropics region in Queensland to southern New South Wales, and has previously been recorded from the Eungella region (Baroni Urbani & Andrade, 2003).

Pseudomyrmecinae (1 genus, 1 species)

A single specimen of *Tetraponera punctulata* was collected from a Malaise trap at one of the 600 m asl sites. *Tetraponera punctulata* is the most widespread Australian species of the genus, occurring across most of the continent except the extreme south and parts of the arid interior (Ward, 2001). It mostly inhabits woodlands and open forests, but has been collected in rainforest in Queensland and Papua New Guinea (Ward, 2001). Species of *Tetraponera* are lignicolous, nesting arboreally in hollows in twigs and branches (Ward, 2001).

General Discussion

In total we collected at least 142 species of ants across the Eungella elevational gradient of 200 to 1200 m asl, which comprised a total of 34 sites each sampled between one and three times. Here we compare the total species pools recorded on our Lamington (20 sites from 300–1100 m asl) and Mt Lewis gradients (20 sites from 400–1200 m asl), but quantitative analysis is difficult due to the variation in sampling intensities and the extent of the elevational gradients. Sampling intensity at our Wet Tropics gradient (a single survey) was too low for meaningful comparison with the two more southerly gradients. Sampling intensity at the Lamington gradient was at least comparable, where a similar total of 145 ant species was recorded using the same sampling methods on three separate surveys (143 species noted in Burwell & Nakamura, 2011, but more careful sorting yielded additional species). As ant species richness typically declines with increasing latitude (Dunn *et al*., 2009), the more tropical Eungella gradient would be expected to be more diverse, but our results suggest that the more southerly Lamington gradient may have a larger species pool. However, when comparisons were made on the basis of a single survey in the same season, species richness declined with increasing latitude from Mt Lewis to Eungella to Lamington (Burwell & Nakamura, 2016), although, as noted above, the Eungella gradient spanned a greater range of elevations with more sites.

Comparing the total numbers of species collected at sites within each band of elevation along the gradient,

species richness peaked at 600 m asl at Eungella, with monotonic declines in species richness with increasing and decreasing elevation (Figure 1) from 600 m. In contrast, at Lamington, species richness peaked at the lowest elevation and monotonically declined with increasing elevation (Figure 1; and see Burwell & Nakamura, 2011). Comparisons of total species richness at each elevation at Eungella (and Lamington) are also confounded by unequal numbers of sites sampled differing numbers of times, with more sites and total site surveys particularly at 400, 600 and 800 m asl (Table 1). When correcting for sampling intensity across the two gradients, Burwell & Nakamura (2016) found broadly similar patterns, richness peaking at mid-elevations at Eungella and at the lowest elevations at Lamington. They suggested that the lower richness at lower elevations at Eungella may be due to historical lowland biotic attrition (Burwell & Nakamura, 2016).

We found progressive turnover in ant species composition with increasing elevation at Eungella. There appeared to be, however, two different gradients of turnover in the ant fauna, one from 200 to 600 m asl and the other from 800 to 1200 m asl. Assemblages of moth species sampled with light traps along the same elevational gradient were similarly divided into lowland and upland assemblages, as were assemblages of tree species (Odell *et al*., 2016). Tree species composition is likely to strongly influence the species composition of herbivorous Lepidoptera; however, it is unlikely to drive ant assemblages to the same extent. Nowrouzi *et al*. (2016) found similar patterns of compositional disjunction between 600 and 800 m asl in a number of subregions within the Australian Wet Tropics, including the Carbine Uplands where our Mt Lewis gradient is located. This zone of disjunction coincided with a strong environmental threshold of seasonal stability in moisture associated with cloud 'stripping' (Nowrouzi *et al*., 2016). Given that the upland rainforests of the Eungella plateau are a northern outlier of subtropical rainforest (Weber *et al*., 2013), long-term climate stability may well underlie the difference in the ant fauna of the uplands in Eungella, as suggested for the Wet Tropics by Nowrouzi *et al*. (2016).

A number of factors may drive the apparent differences in composition between the ant faunas of the lowlands and highlands at Eungella: greater numbers of tropical species in the lowlands and, conversely, greater numbers of subtropical species in the highlands; and a greater representation of arboreal-nesting species in the lowlands compared with the highlands. Many primarily tropical ant species were collected only from sites from 200 to 600 m asl at Eungella, and likely contributed to differences between the lowland and upland ant faunas of the region. Some ground- and litter-inhabiting species demonstrated this distribution pattern including, for example, *Zasphinctus turneri* (Dorylinae), *Acropyga acutiventris* (Formicinae) and *Strumigenys guttulata*, *Pristomyrmex foveolatus* and *Calyptomyrmex fragarus* (Myrmicinae) (Table 2). In particular, in the lowlands, there was a substantially greater representation of species nesting and foraging arboreally, compared with the highlands. This was the case for multiple genera and subfamilies: for example, *Tapinoma* and *Turneria* (Dolichoderinae); *Colobopsis*, *Echinopla*, *Oecophylla*, and the *Polyrhachis* subgenera *Campomyrma* and *Hedomyrma* (Formicinae); *Crematogaster* and *Podomyrma* (Myrmicinae); and *Platythyrea* (Ponerinae).

The higher elevations at Eungella, and in particular the rainforests at 1000 and 1200 m asl, featured a number of subtropical species that also occurred at our Lamington gradient. In many cases, but not all, Eungella represents the northernmost extent of their known geographic ranges. A number of subfamilies contained taxa fitting this distributional pattern. Notable examples included: *Amblyopone hackeri* (Amblyoponinae); *Anonychomyrma* QM.3 (Dolichoderinae); *Rhytidoponera chalybaea* (Ectatomminae); *Myrmecorhynchus emeryi* and *Prolasius convexus* (Formicinae); *Monomorium 'leae'* and *Monomorium kiliani* (Myrmicinae). Also recorded only from 1000 and 1200 m asl in our surveys were two species, *Myrmecia eungellensis* and an undescribed species of *Notoncus*, that appear to be endemic to the Eungella region, or at least the Clarke Range. A second species of *Myrmecia*, *M. fabricii*, may also be restricted to the high elevations of the Eungella region, but there are some questions regarding its validity as a species distinct from *M. eungellensis*. *Orectognathus parvispinus* is also currently known only from the Eungella region, but occurs at somewhat lower elevations, 400–800 m asl.

Comparing the observed elevational ranges of species that occurred at both the Eungella (21.1°S) and Lamington (28.1°S) gradients, we found inconsistent responses to the approximately 7° difference in latitude between the gradients. However, as would be predicted, at least some species had higher elevational ranges at Eungella than at Lamington. Species that showed relatively high site and temporal fidelity across both gradients provided the more convincing examples, which involved upslope shifts of both lower and/or

upper range margins at Eungella. Examples of lower range margin shifts included *Monomorium 'leae'* (300–1100 m at Lamington versus 800–1200 m at Eungella) and *Anonychomyrma* QM.3 (300–1100 m at Lamington versus 800–1200 m at Eungella), whereas *Myrmecorhynchus emeryi* appeared to show a shift in its upper range margin (500–900 m at Lamington versus 600–1200 m at Eungella). The upper and lower range margins of *Orectognathus versicolor* differed between transects (300–900 m at Lamington versus 800–1200 m at Eungella). *Rhytidoponera chalybaea* showed a similar pattern, occurring at 300–700 m at Lamington versus 1000–1200 m at Eungella. At Eungella, the potential influence of the closely related *R. impressa* on the lower range margin of *R. chalybaea* is worthy of attention, given that *R. impressa* replaced *R. chalybaea* at 800 m asl. With the exception of *R. chalybaea*, many of the species listed above seem to track their climatic envelopes and are not strongly influenced by other factors such as competition and other habitat conditions. These species are potentially a good predictor set of species to quantify the impacts of future climate change.

In conclusion, the ant fauna of the Eungella region appears to be an amalgam of different faunal elements. Rainforest ants from the lowlands include a greater representation of tropical elements, including a number of species whose distributional ranges extend only as far south as the Clarke Range. In addition, a greater number of arboreal-nesting species, including weavers and lignicolous species, are found in the lowlands. The ant fauna of the upland rainforest has a greater representation of largely subtropical ant species, many of which do not occur farther north than the Clarke Range. At least some ant species, two species of *Myrmecia*, *Orectognathus parvispinus* and an undescribed species of *Notoncus*, appear to be restricted to the Eungella region, or at least the wider Clarke Range. The ant fauna of our Eungella elevational gradient represents an ecotone of tropical and subtropical elements. The distributional patterns of ants at Eungella clearly demonstrate that this area is highly significant in terms of conservation. The baseline information presented here, in combination with ongoing monitoring, will be useful in quantifying the ecological impacts of future climatic change.

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LITERATURE CITED

ANTWEB. Available from https://www.antweb.org/. Accessed November 2018.

Ashton, L. A., Odell, E. H., Burwell, C. J., Maunsell, S. C., Nakamura, A., McDonald, W. J. F. & Kitching, R. L. (2016). Altitudinal patterns of moth diversity in tropical and subtropical Australian rainforests. *Austral Ecology* **41**, 197–208.

Baroni Urbani, C. (1977). Materiali per una revisione della sottofamiglia Leptanillinae Emery (Hymenoptera: Formicidae). *Entomologica Basiliensia* **2**, 427–488.

Baroni Urbani, C. & De Andrade, M. L. (2003). The ant genus *Proceratium* in the extant and fossil record. *Museo Regionale di Scienze Naturali Monografie (Turin)* **36**, 1–492.

Blaimer, A. A., Lapolla, J. S., Branstetter, M. G., Lloyd, M. W. & Brady, S. G. (2016). Phylogenomics, biogeography and diversification of obligate mealybug-tending ants in the genus *Acropyga*. *Molecular Phylogenetics and Evolution* **102**, 20–29.

Bolton, B. (2007). Taxonomy of the dolichoderine ant genus *Technomyrmex* (Hymenoptera: Formicidae) based on the worker caste. *Contributions of the American Entomological Institute* **35**, 1–149.

Brown, W. L., Jr. (1975). Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogitini. *Search Agriculture (Ithaca N. Y.)* **5**(1), 1–115.

Burwell, C. J. & Nakamura, A. (2011). Distribution of ant species along an altitudinal transect in continuous rainforest in subtropical Queensland, Australia. *Memoirs of the Queensland Museum – Nature* **5**, 391–411.

Burwell, C. J. & Nakamura, A. (2016). Can changes in ant diversity along elevational gradients in tropical and subtropical Australian rainforests be used to detect a signal of past lowland biotic attrition? *Austral Ecology* **41**, 209–218.

Delsinne, T., Sonet, G., Nagy, Z. T., Wauters, N., Jacquemin, J. & Leponce, M. (2012). High species turnover of the ant genus *Solenopsis* (Hymenoptera: Formicidae) along an altitudinal gradient in the Ecuadorian Andes, indicated by a combined DNA sequencing and morphological approach. *Invertebrate Systematics* **26**, 457–469.

Dunn, R. R., Agosti, D., Andersen, A. N., Arnan, X., Bruhl, C. A., Cerda, X., Ellison, A. M., Fisher, B. L., Fitzpatrick, M. C., Gibb, H., Gotelli, N. J., Gove, A. D., Guenard, B., Janda, M., Kaspari, M. E., Laurent, E. J., Lessard, J-P., Longino, J. T., Majer, J. D., Menke, S. B., McGlynn, T. P., Parr, C. L., Philpott, S. M., Pfeiffer, M., Retana, J., Suarez, A. V., Vasconcelos, H. L., Weiser, M. D. & Sanders, N. J. (2009). Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecology Letters* **12**, 324–333.

Heterick, B. E. (2001). Revision of the Australian ants of the genus *Monomorium* (Hymenoptera: Formicidae). *Invertebrate Taxonomy* **15**, 353–459.

Heterick, B. E. & Shattuck, S. (2011). Revision of the ant genus *Iridomyrmex* (Hymenoptera: Formicidae). *Zootaxa* **2845**, 1–174.

Kohout, R. J. (2000). A review of the distribution of the *Polyrhachis* and *Echinopla* ants of the Queensland Wet Tropics (Hymenoptera: Formicidae: Formicinae). *Memoirs of the Queensland Museum* **46**, 183–209.

Lapolla, J. (2004). *Acropyga* (Hymenoptera: Formicidae) of the world. *Contributions of the American Entomological Institute* **33**, 1–130.

Lapolla, J. S., Burwell, C., Brady, S. G., Miller, D. R. (2008). A new ortheziid (Hemiptera: Coccoidea) from Australia associated with *Acropyga myops* Forel (Hymenoptera: Formicidae) and a key to Australian Ortheziidae. *Zootaxa* **1946**, 55–68.

Lucky, P. S. & Ward, P. S. (2010). Taxonomic revision of the ant genus *Leptomyrmex* Mayr (Hymenoptera: Formicidae). *Zootaxa* **2688**, 1–67.

Mezger, D. & Moreau, C. S. (2016). Out of South-East Asia: phylogeny and biogeography of the spiny ant genus *Polyrhachis* Smith (Hymenoptera: Formicidae). *Systematic Entomology* **41**, 369–378.

Nowrouzi, S., Andersen, A. N., Macfadyen, S., Staunton, K. M., Vanderwal, J. & Robson, S. K. A. (2016). Ant diversity and distribution along elevation gradients in the Australian Wet Tropics: the importance of seasonal moisture stability. *PLoS ONE* **11**, e0153420.

Odell, E. H., Ashton, L. A. & Kitching, R. L. (2016). Elevation and moths in a central eastern Queensland rainforest. *Austral Ecology* **41**, 133–144.

Ogata, K. & Taylor, R. W. (1991). Ants of the genus *Myrmecia* Fabricius: a preliminary review and key to the named species (Hymenoptera: Formicidae: Myrmeciinae). *Journal of Natural History* **25**, 1623–1673.

Shattuck, S. O. (1990). Revision of the dolichoderine ant genus *Turneria* (Hymenoptera: Formicidae). *Systematic Entomology* **15**, 101–117.

Shattuck, S. O. (1993). Revision of the *Iridomyrmex calvus* species-group (Hymenoptera: Formicidae). *Invertebrate Taxonomy* **7**, 1303–1325.

Shattuck, S. O. (1999). *Australian Ants. Their Biology and Identification*. Monographs on Invertebrate Taxonomy 3, CSIRO Publishing, Collingwood, Victoria.

Shattuck, S. O. (2008). Revision of the ant genus *Prionopelta* in the Indo-Pacific region. *Zootaxa* **1846**, 21–34.

Shattuck, S. (2009). A revision of the Australian species of the ant genus *Myrmecina* (Hymenoptera: Formicidae). *Zootaxa* **2146**, 1–21.

Shattuck, S. O. (2011). Revision of the ant genus *Calyptomyrmex* (Hymenoptera: Formicidae) in South-east Asia and Oceania. *Zootaxa* **2743**, 1–26.

Shattuck, S. O. (2015). A review of the ant genus *Myrmecorhynchus* (Hymenoptera: Formicidae). *Zootaxa* **3955**, 283–290.

Taylor, R. W. (1965). The Australian ants of the genus *Pristomyrmex*, with a case of apparent character displacement. *Psyche* **72**, 35–54.

Taylor, R. W. (1977). New ants of the Australasian genus *Orectognathus*, with a key to the known species (Hymenoptera: Formicidae). *Australian Journal of Zoology* **21**, 581–612.

Taylor, R. W. (1988). The nomenclature and distribution of some Australian and New Caledonian ants of the genus *Leptogenys* Roger (=*Prionogenys* Emery, n. syn.) (Hymenoptera: Formicidae: Ponerinae). *General and Applied Entomology* **20**, 33–37.

Taylor, R. W. (1992). Nomenclature and distribution of some Australian and New Guinean ants of the subfamily Formicinae (Hymenoptera: Formicidae). *Journal of the Australian Entomological Society* **31**, 57–69.

Taylor, R. W. (2011). Australasian ants of the subfamily Heteroponerinae (Hymenoptera: Formicidae): (1) General introduction and review of the *Heteroponera leae* (Wheeler, 1923) species group, with descriptions of two new species. *Myrmecological News* **15**, 117–123.

Taylor, R. W. (2015). Australasian ants of the subfamily Heteroponerinae (Hymenoptera: Formicidae): (2) the species-group of *Heteroponera relicta* (Wheeler) with descriptions of nine new species and observations on morphology, biogeography and phylogeny of the genus. *Zootaxa* **3947**, 151–180.

Wang, M. (2003). A monographic revision of the ant genus *Pristomyrmex* (Hymenoptera: Formicidae). *Bulletin of the Museum of Comparative Zoology* **157**, 383–539.

Ward, P. S. (1980). A systematic revision of the *Rhytidoponera impressa* group (Hymenoptera: Formicidae) in Australia and New Guinea. Australian *Journal of Zoology* **28**, 475–498.

Ward, P. S. (2001). Taxonomy, phylogeny and biogeography of the ant genus *Tetraponera* (Hymenoptera: Formicidae) in the Oriental and Australian regions. *Invertebrate Taxonomy* **15**, 589–665.

Ward, P. S., Brady, S. G., Fisher, B. L. & Schultz, T. R. (2015). The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). *Systematic Entomology* **40**, 61–81.

Ward, P. S., Blaimer, B. B. & Fisher, B. L. (2016). A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera *Colobopsis* and *Dinomyrmex*. *Zootaxa* **4072**, 343–357.

Ward, P. S. & Fisher, B. L. (2016). Tales of dracula ants: the evolutionary history of the ant subfamily Amblyoponinae (Hymenoptera: Formicidae). *Systematic Entomology* **41**, 683–693.

Weber, L. C., Vanderval, J., Schmidt, S., McDonald, W. J. F. & Shoo, L. P. (2013). Patterns of rain forest plant endemism in subtropical Australia relate to stable mesic refugia and species dispersal limitations. *Journal of Biogeography* **4**, 222–38.

Wetterer, J. K. (2017). Geographic distribution of the weaver ant *Oecophylla smaragdina*. *Asian Myrmecology* **9**, e009004: 1–12.