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Altitudinal variation of parasitic Hymenoptera assemblages in Australian subtropical rainforest

Casey R Hall,[1]* Chris J Burwell,[1,2] Akihiro Nakamura[3] and Roger L Kitching[1]

[1]*Environmental Futures Research Institute and Griffith School of Environment, Griffith University, Nathan, Qld. 4111, Australia.*
[2]*Natural Environments Program, Queensland Museum, South Brisbane, Qld. 4101, Australia.*
[3]*Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, China.*

Abstract Patterns of species assemblages along altitudinal gradients provide insights into ecological patterns and processes. Parasitoids play an important role in ecosystems, yet there are few studies on parasitoid assemblages, partly because of difficulty in identification of parasitoids to species or their surrogates, morphospecies. The aim of this study is to assess differences in assemblages of parasitic Hymenoptera along an altitudinal gradient at both the family and morphospecies level, and the potential of environmental variables for explaining these differences. We sampled from four replicate sites at each of five elevations (approximately 300, 500, 700, 900 and 1100 m above sea level (asl)) within continuous subtropical rainforest of the Border Ranges National Park in New South Wales, Australia. At each site, we operated a Malaise trap for 10 days in December 2011 and again in February 2012. Parasitic wasps were sorted to families, and two of the common families (Diapriidae and Ichneumonidae) were further sorted to morphospecies. At both family and morphospecies level, we found gradual altitudinal turnover with a clear separation between 'upland' (900 and 1100 m asl) and 'lowland' (300 and 500 m asl) assemblages. Unlike parallel studies of some other major taxa, we did not detect distinct assemblages at each altitude at the taxonomic resolution used. In addition, response patterns were different between the two sampling occasions. Changes in assemblage composition were best explained by either altitude or temperature. Although parasitic Hymenoptera do not respond as clearly to changes in altitude as some other taxa, the changes detected here, even at the family level, are important given the role parasitoids play in ecosystem functioning.

Key words community pattern, elevation, parasitoid, taxonomic level, temperature.

INTRODUCTION

Altitudinal gradients are ideal natural systems for studying ecological patterns and how communities respond to a range of climates over a relatively small spatial scale (Grytnes & McCain 2007; Kitching *et al*. 2011). In consequence, studies carried out along altitudinal gradients can be useful in predicting how species and communities may respond to future changes in climate through changes in their distributions (Fielding *et al*. 1999; Hodkinson 2005). Insects represent a large proportion of terrestrial diversity, yet relatively little is known about their altitudinal distributions (Brehm *et al*. 2007). This is especially true in Australia, which lacks the long-term monitoring of species' distributions that exists for some locations in the northern hemisphere (Hughes 2003). The 'IBISCA Queensland' project attempted to address this shortfall by documenting the distributions of a range of invertebrate groups along an altitudinal gradient in subtropical rainforest of south-east Queensland (Kitching *et al*. 2011).

Distinct changes in assemblage composition of ants (Burwell & Nakamura 2011) and moths (Ashton *et al*. 2011) accompanied changes in altitude along the IBISCA-Queensland gradient. In addition, significant correlations of assemblage composition with altitude have been found in various insect groups in tropical rainforests, including ants (Longino & Colwell 2011), flies (Wilson *et al*. 2007), moths (Brehm & Fiedler 2003) and dung beetles (Escobar *et al*. 2005). Among these studies, altitudinal changes in environmental factors, such as climate, are cited as the most important driver of assemblage turnover with altitude. Brehm and Fiedler (2003), however, proposed that the observed faunal changes in geometrid moths with altitude was likely due to expected host plant distributions, which in turn are influenced by environmental factors. More recently, the size of the regional species pool has been suggested as the main driver of beta diversity patterns along altitudinal gradients (Kraft *et al*. 2011). Most

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*casey.hall@griffith.edu.au

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evidence, however, shows climatic factors as the main proximal drivers of altitudinal distributions (Hodkinson 2005; McCain 2007). Temperature, precipitation and humidity change more or less predictably with altitude, and these differences generate the ecological patterns found along altitudinal gradients (Escobar *et al*. 2005).

Parasitoids, with their high trophic position and high degree of host specificity, are particularly sensitive to environmental changes (Siemann 1998; Tscharntke *et al*. 1998). In addition, they play an important role in ecosystems because of the sheer number of interactions involving parasitoids and their ability to regulate host populations (Price 1980; Strong *et al*. 1984). Despite their ecological importance, we have only a basic knowledge of how parasitoid assemblages change along habitat gradients and which environmental factors may drive these changes. Of the few altitudinal studies on parasitoid communities, Kaufman and Wright (2011) found that altitude explained a significant amount of variation in assemblage structure of *Udea stellata* (Lepidoptera) parasitoids, although host density and habitat disturbance explained a greater proportion of variation. Maunsell (2014), however, found no relationship between altitude and the assemblage structure of leaf miner parasitoids. Most altitudinal studies on parasitoids report only on patterns of species richness, with mid-altitudinal peaks the most commonly reported pattern (Janzen & Pond 1975; Gauld 1985; Noyes 1989; McCoy 1990). However, Peck *et al*. (2008) found that species richness of Ichneumonoidea increased with elevation.

In the present study, we examined altitudinal patterns of assemblage composition of parasitic Hymenoptera at the family and morphospecies level. Family-level analysis has been proposed as a useful method for investigating large-scale ecological patterns (Kitching *et al*. 2004) as it is less labour intensive, time consuming and costly compared with a species-level approach (Pik *et al*. 1999). Family-level taxonomic resolution has been used successfully to describe patterns in invertebrate assemblage composition in flies (Kitching *et al*. 2004), and bees and wasps (Arnan *et al*. 2011). While family-level identification may be sufficient to detect strong ecological patterns, species-level sorting may be required to detect subtle changes in assemblage structure (Grimbacher *et al*. 2008). The use of morphospecies requires less taxonomic expertise than species identification, although without prior training this method can lead to large errors (Derraik *et al*. 2010). It is, however, still a valuable tool for finding patterns, particularly in taxonomically neglected taxa, and can provide very similar results to formal species identification when applied with care (Oliver & Beattie 1996; Pik *et al*. 1999; Krell 2004).

We aimed to assess differences in the assemblages of parasitic Hymenoptera along an altitudinal gradient within subtropical rainforest and the potential of environmental variables for explaining these differences. We first examined patterns at the family level of the whole parasitoid wasp community, and then at the morphospecies level within the families Ichneumonidae and Diapriidae.

MATERIALS AND METHODS

Study area

The study sites were located in continuous subtropical rainforest along an altitudinal gradient within the Border Ranges National Park (28°23’S, 153°03’E) in north-east New South Wales, Australia. Border Ranges National Park comprises 31 683 ha, ranging in elevation from approximately 300 to 1100 m. The region has a subtropical climate with distinct seasonal rainfall in spring and summer, with a mean annual rainfall of 1800 mm (measured at O’Reilly’s Alert, 913 m above sea level (asl) (station number 40931), Australian Bureau of Meteorology 2011). The vegetation below 800 m is subtropical rainforest, classified by Webb and Tracey (1981) as complex notophyll vine forest, with *Argyrodendron* spp. as the dominant canopy trees. Cool temperate rainforest (microphyll fern forest) is found above 900 m and is restricted to cool, misty sites with high direct and occult rainfall, and is dominated by *Nothofagus moorei* (McDonald 2010).

Our survey sites were located within broad altitudinal categories centred around 300, 500, 700, 900 and 1100 m asl (see Appendix I for site coordinates and environmental attributes). Each altitude had four replicate 20 m by 20 m plots. Sites within each altitude were separated by at least 400 m.

Parasitic Hymenoptera sampling

Townes design Malaise traps (Townes 1962) were used to sample insects at the 20 sites along the altitudinal transect. A single Malaise trap, with a collecting jar filled with at least 500 mL of 70% ethanol as the killing agent, was set up at the centre of each site for 10 consecutive days in December 2010 and again in February 2011; thus, each site was sampled for a total of 20 days. All parasitic Hymenoptera were removed from samples and stored in 70% ethanol. This study was limited to families within the ‘Parasitica’ (i.e. all Hymenoptera: Apocrita except the Chrysidoidea, Vespoidea and Apoidea). Parasitoids were identified to family following Naumann (1991) and Stevens *et al*. (2007) by CRH except for the Chalcidoidea, which were sorted to family by CJB. The Ichneumonidae and Diapriidae were sorted to morphospecies by CRH following Naumann (1982) and Gauld (1984), with prior taxonomic training given by CJB. Although morphospecies sorting was checked by CJB, there remains the possibility of minor errors due to cryptic species and sexual dimorphism. Voucher specimens were mounted and are deposited in the Arthropod Biodiversity Laboratory at Griffith University. The Ichneumonidae and Diapriidae were chosen for their high diversity and their considerable differences in body size and host taxa. Ichneumonidae is estimated to comprise more than 1500 species in Australia of which 433 are described (Stringer *et al*. 2011). They range in length from 1.5 to 120 mm and attack many endopterygote insect hosts, although the most common host taxon are the Lepidoptera (Gauld 1984; Naumann 1991). In contrast, the Diapriidae has an estimated 500 species in Australia of which 149 are

Table 1 Environmental variables measured at each of the 20 sampling sites with average values, where appropriate, for each elevational band

Variable	Description	Mean (SE)				
		300	500	700	900	1100
Slope	Clinometer measurements converted to degrees	12 (1.7)	19 (2.6)	23 (1.3)	21 (3.6)	10 (1.0)
Leaf litter depth (cm)	Average of 10 vertical ruler measurements	1.4 (0.2)	1.1 (0.2)	1.2 (0.2)	1.1 (0.2)	1.7 (0.1)
Fallen dead wood (cm)	Sum of diameters of dead wood ≥5 cm intersecting a 20 m transect	75 (21)	78 (31)	67 (19)	95 (16)	49 (13)
Canopy cover (%)	Average of 10 canopy scope readings	84 (0.5)	79 (2.7)	86 (1.8)	84 (2.2)	81 (3.8)
Aspect	Compass bearing converted to Cartesian coordinates where north is 1, south −1, east 1 and west −1	W	SW	SW	SW	S
Area (%)	Estimate of forested area in each 100 m elevation band within 50 km^2 of gradient (as per Kluge *et al.* 2006)	5.0	8.3	16.3	18.8	2.7
Tree species richness	Total number of tree species within 20 × 20 m plot	19 (2.6)	16 (1.9)	21 (2.2)	25 (2.6)	17 (1.3)
Vegetation PCO1	primary PCO axis of the tree species resemblance matrix					
Temperature (°C)	Average of hourly measurements from April 2010 to April 2011 (*DS21* Thermochron® iButton®, Maxim, CA, USA)	15.5 (0.1)	14.9 (0.2)	13.4 (0.1)	12.5 (0.0)	12.0 (0.1)
Altitude (m asl)	GPS reading, Garmin eTrex®	308 (7)	484 (10)	705 (5)	906 (13)	1050 (6)

PCO, principal coordinate.

described (Stringer *et al.* 2012). They are small (1–6 mm) and what is known about their biology suggests that they mostly parasitise dipteran larvae (Naumann 1982, 1991).

Habitat survey

A range of environmental variables were measured at each site (Table 1). We measured leaf litter depth, amount of dead wood on the ground and canopy cover as studies have shown that habitat complexity can influence parasitoid community structure (Lassau & Hochuli 2005). We also measured the available area within each altitudinal band as area typically declines with increasing altitude, and this may influence species richness (Rahbek 1995). Slope and aspect of each site were also measured.

In parallel with this study, John Hunter and Stephanie Horton (National Parks and Wildlife NSW) and Bill McDonald (Queensland Herbarium) conducted vegetation surveys at each site using the protocols of Laidlaw *et al.* (2012). A principal coordinate analysis (PCO) was performed on a matrix of Bray–Curtis similarity distances between pairs of sites based on $\ln(x + 1)$ transformed tree species abundances, using the PERMANOVA+ package in PRIMER 6 (Clarke & Gorley 2006; Anderson *et al.* 2008). The primary PCO axis of the tree species resemblance matrix (PCO1) explained a large amount of the total variation (33%). Subsequently, scores from this axis were used as an index of tree species composition in further analysis of the insect data.

Analysis

The December 2010 and February 2011 datasets were analysed separately to avoid sampling occasion confounding altitudinal patterns. We tested for the effect of altitude on parasitoid assemblage composition using the permutational multivariate ANOVA (PERMANOVA) procedure available in the PERMANOVA+ package in PRIMER 6 (Clarke & Gorley 2006; Anderson *et al.* 2008). Abundance data were square root transformed to reduce the influence of dominant families or morphospecies. A resemblance matrix using Bray–Curtis similarities was created for each transformed abundance dataset (Bray & Curtis 1957). Pseudo-F and *P*-values were calculated using 4999 unrestricted permutations of data. The resulting *P*-values were used to determine if significant differences ($\alpha = 0.05$) in assemblage composition occurred with altitude. Permutation-based *post hoc* pair-wise comparisons were conducted between grouped low-altitude (300 and 500 m) and high-altitude sites (900 and 1100 m). Non-metric multidimensional scaling (NMDS) ordinations were created to visualise the response of parasitoid assemblage structure to altitude. Vector overlays of families or morphospecies correlated with the NMDS ordination (Pearson correlation > 0.75) were also created.

We assessed the potential of the environmental variables from Table 1 to explain patterns of parasitoid assemblage composition using a distance-based linear model (DistLM) routine in PERMANOVA+ (McArdle & Anderson 2001; Anderson *et al.* 2008). Marginal tests were used to investigate the relationship between assemblages and all environmental variables individually. The model that best explained the variation in parasitoid assemblages was then selected using a step-wise selection procedure based on the Akaike information criterion, adjusted for finite sample sizes (AICc) (Anderson *et al.* 2008). The results need to be interpreted with caution as altitude, mean temperature and PCO1 of tree species assemblages were highly correlated with each other ($r > 0.9$). Because 11 environmental variables were tested, a Bonferroni-adjusted critical significance level of 0.0045 was used to compensate for the increased probability of type-I error.

RESULTS

Parasitoid family-level assemblages

Sampling in December 2010 and February 2011 yielded a total of 8640 individual parasitoid wasps belonging to 21 families and 7 superfamilies (Appendix II). Total abundance was similar between sampling occasion, with December and February accounting for 48% and 52% of total abundance, respectively. The most abundant family was Diapriidae (3761 individuals), followed by Braconidae (1367), Scelionidae (974), Platygasteridae (879) and Ichneumonidae (592). Combined, these five families represented 87% of all sampled specimens.

Both sampling months showed similar trends in the change in relative abundance of the dominant families with altitude (Fig. 1). Diapriidae became increasingly dominant with increasing altitude, accounting for over 75% (December) and 55% (February) of all parasitoids at 1100 m, whereas the relative abundances of most other families decreased with altitude (Fig. 1). However, total parasitoid abundance declined with increasing altitude in December, whereas abundance increased with increasing altitude in February (Table 2).

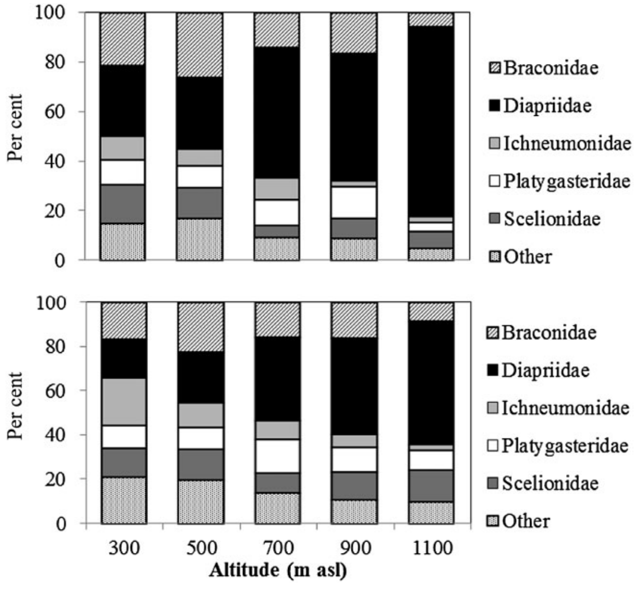


Fig. 1. Relative abundance of the five most abundant parasitic Hymenoptera families collected in Malaise traps ($n = 4$) at each altitude in December 2010 (upper) and February 2011 (lower).

Family-level NMDS ordinations for both December and February displayed gradual change across the altitudinal gradient with lower altitude (300 and 500 m) assemblages generally clearly separated from higher altitude (900 and 1100 m) assemblages (Fig. 2a,b). In December, low to mid (700 m) altitude sites were relatively tightly clustered while 900 m and 1100 m sites were more dispersed (Fig. 2a). However, the reverse pattern occurred in February (Fig. 2b). Six families were strongly correlated (Pearson correlation > 0.75) with the December and February ordinations, although only Diapriidae, Ichneumonidae and Braconidae were strongly correlated on both occasions (Fig. 2a,b). Significant differences in assemblage composition among altitudes were confirmed by PERMANOVA for both December and February (Table 3a). *Post hoc* pair-wise comparisons showed that low-altitude sites (300 and 500 m) had significantly different assemblages from high-altitude sites (900 and 1100 m) in both December and February (Table 3b).

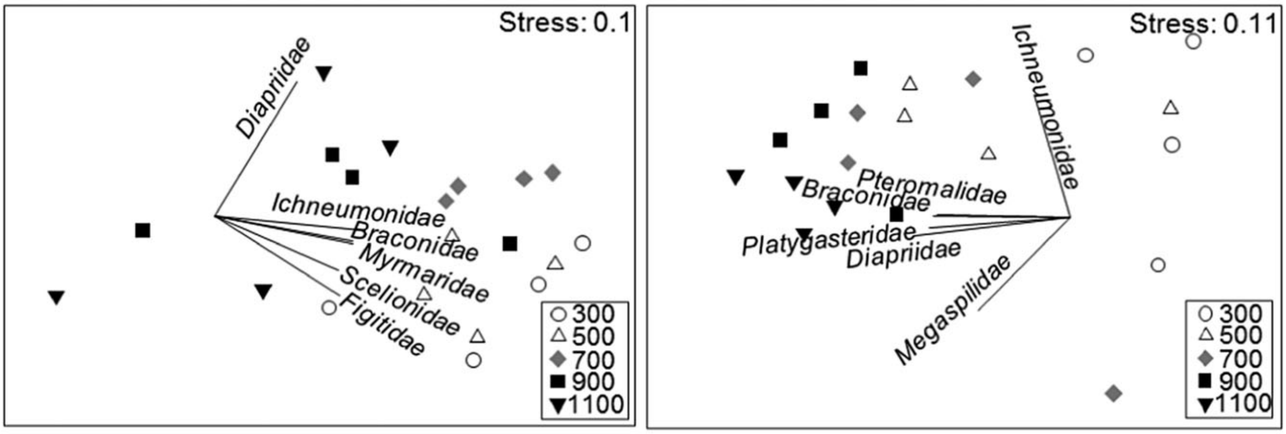
Ichneumonidae and Diapriidae assemblage composition

Diapriidae were the most abundant family with 3761 individuals representing 47 morphospecies, whereas the Ichneumonidae were substantially less abundant (592 individuals) but more speciose, with 71 morphospecies (Appendix III). The Ichneumonidae were characterised by a high number (44% of total) of morphospecies represented by a single specimen (‘singletons’), whereas there were very few singletons in the Diapriidae (four species, 9%) (Appendix III). Ichneumonidae were least abundant at 1100 m and the Diapriidae at 300 m (Table 2). No Ichneumonidae were collected from one of the 900 m and one of the 1100 m sites in December, resulting in fewer degrees of freedom in the PERMANOVA analysis.

Unlike the family-level analyses, assemblages of ichneumonid morphospecies did not show clear groupings of low- and high-altitude sites in the NMDS ordinations (Fig. 2c,d). The effect of altitude was significant, however, in both December and February (Table 3a). Results of *post hoc* pair-wise comparisons showed that low-altitude sites (300 and 500 m) had significantly different assemblages from high-altitude sites (900 and 1100 m) in both December and February (Table 3b). No single morphospecies was correlated with the pattern of ichneumonid assemblages at a cut-off value of >0.75 of Pearson’s correlation coefficient.

Table 2 Average abundances of all parasitic Hymenoptera (total) and of Ichneumonidae and Diapriidae collected in Malaise traps ($n = 4$) at each altitude in December (2010) and February (2011)

Site	Total (SE)		Ichneumonidae (SE)		Diapriidae (SE)	
	December	February	December	February	December	February
300	239.5 (75.1)	67.5 (8.2)	23.0 (5.2)	14.0 (4.7)	67.5 (27.2)	11.8 (3.2)
500	216.3 (55.2)	158.3 (39.2)	15.0 (4.2)	17.3 (3.0)	63.0 (17.2)	35.8 (9.2)
700	297.3 (42.6)	191.8 (54.2)	25.5 (4.3)	17.0 (7.8)	156.8 (20.8)	71.3 (26.1)
900	162.3 (48.0)	298.8 (64.4)	4.3 (3.0)	17.3 (6.7)	83.0 (20.9)	130.0 (29.5)
1100	123.3 (41.0)	405.5 (72.6)	3.3 (1.4)	10.8 (1.9)	95.8 (37.0)	231.0 (53.6)



(a) Family-level December

(b) Family-level February

(c) Ichneumonidae December

(d) Ichneumonidae February

(e) Diapriidae December

(f) Diapriidae February

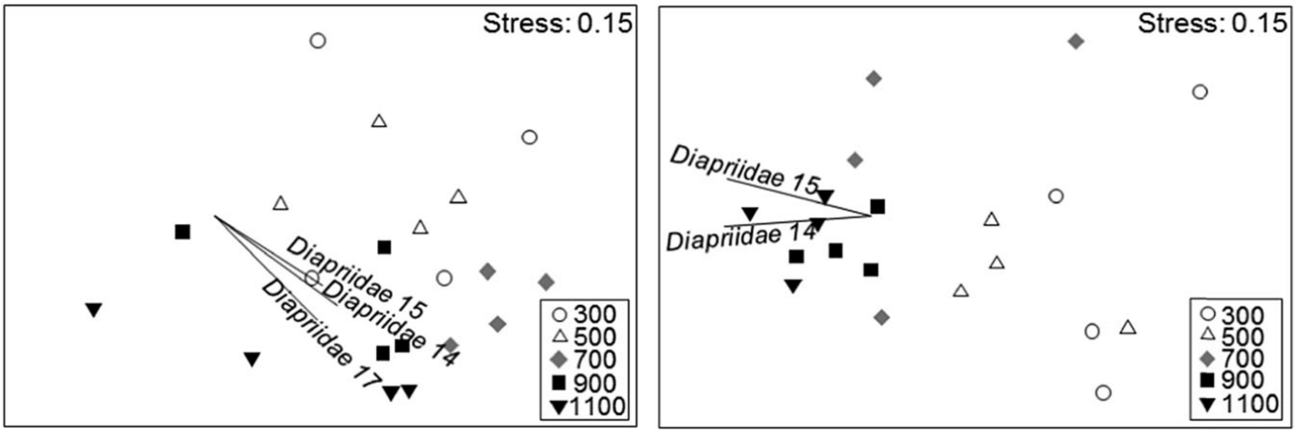


Fig. 2. Ordinations (non-metric multidimensional scaling (NMDS)) of parasitoid assemblages from each site based on square root transformed abundances and Bray–Curtis distances: at the family level for (a) December and (b) February; and at the morphospecies level for the Ichneumonidae in (c) December and (d) February, and the Diapriidae in (e) December and (f) February. Families or species highly correlated with each NMDS ordination (Pearson correlation >0.75) are shown as vectors.

Diapriid assemblage composition changed significantly with altitude in both December and February (Table 3a). As was the case for family-level assemblages, the NMDS ordination of diapriid morphospecies showed gradual change across the altitudinal gradient, with low-altitude assemblages separated from high-altitude assemblages in both December and February (Fig. 2e,f). *Post hoc* pair-wise comparisons showed that diapriid assemblages from the two lower altitudes were significantly different from the two higher altitudes (Table 3b). Three morphospecies, Diapriidae 14, 15 and 17, were positively correlated (Pearson correlation >0.75) with the higher altitudinal categories in December,

Table 3 Summary of (a) PERMANOVA multivariate tests on parasitoid family level, Ichneumonidae and Diapriidae assemblages among altitudes and (b) *P*-values of *post hoc* pair-wise tests comparing differences in assemblage composition between low (300 and 500 m asl) and high (900 and 1100 m asl) altitudes

	December			February		
a) General tests	df	Pseudo-F	*P*	df	Pseudo-F	*P*
Family level	19	2.68	**0.006**	19	3.34	**<0.001**
Ichneumonidae	17	1.9	**0.001**	19	1.58	**0.017**
Diapriidae	19	2.05	**0.002**	19	2.83	**0.001**
b) *Post hoc* (High vs. Low)	df	*t*	*P*	df	*t*	*P*
Family level	14	2.45	**0.002**	14	3.14	**<0.001**
Ichneumonidae	12	1.67	**<0.001**	14	1.57	**0.006**
Diapriidae	14	1.77	**<0.001**	14	2.86	**<0.001**

Bold *P*-values show significant comparisons at $\alpha = 0.05$.

Table 4 Summary of DistLM tests on assemblages based on families, and morphospecies of Ichneumonidae and Diapriidae, showing *P*-values and proportions (Prop) of explained variation for marginal tests and *P*-values, AICc values and proportions (Prop) associated with each variable chosen in sequential tests

	Family				Ichneumonidae				Diapriidae			
	December		February		December		February		December		February	
Marginal test	*P*	Prop	*P*	Prop	*P*	Prop	*P*	Prop	*P*	Prop	*P*	Prop
Mean temp	**0.001**	0.26	**<0.001**	0.37	**<0.001**	0.14	**0.003**	0.13	**0.003**	0.14	**<0.001**	0.31
Leaf litter	0.036	0.14	0.294	0.06	0.322	0.06	0.522	0.05	0.784	0.04	0.413	0.05
Canopy	0.711	0.03	0.934	0.02	0.773	0.05	0.720	0.04	0.834	0.03	0.980	0.02
Slope	0.337	0.06	0.468	0.05	0.598	0.05	0.277	0.06	0.715	0.04	0.444	0.05
Aspect N	0.259	0.07	0.847	0.02	0.735	0.04	0.685	0.04	0.336	0.06	0.634	0.04
Aspect E	0.763	0.03	0.589	0.04	0.853	0.04	0.527	0.05	0.097	0.08	0.455	0.05
Dead wood	0.497	0.04	0.532	0.04	0.545	0.05	0.941	0.03	0.433	0.05	0.773	0.03
Altitude	**0.002**	0.25	**<0.001**	0.36	**<0.001**	0.15	**0.004**	0.13	**0.001**	0.16	**<0.001**	0.29
Area	0.439	0.05	0.268	0.06	0.034	0.1	0.117	0.08	0.270	0.06	0.432	0.05
Tree spp	0.487	0.04	0.414	0.05	0.576	0.05	0.472	0.05	0.702	0.04	0.130	0.08
PCO1 axis	**0.003**	0.21	**<0.001**	0.31	**0.001**	0.13	0.009	0.11	0.006	0.13	**<0.001**	0.29
Sequential test	*P* (AICc)	Prop	*P* (AICc)	Prop	*P* (AICc)	Prop	*P* (AICc)	Prop	*P* (AICc)	Prop	*P* (AICc)	Prop
Mean temperature	0.001 (127)	0.26	0.001 (122)	0.37			0.003 (160)	0.13			0.001 (149)	0.31
Altitude					<0.001 (146)	0.15			0.001 (147)	0.16		

Bold terms indicate significant *P*-values (Bonferroni-adjusted) in marginal tests (see text for further explanation).
PCO, principal coordinate.

while only Diapriidae 14 and 15 were correlated in February (Fig. 2).

Relationship of environmental variables and parasitoid assemblages

Marginal tests, which examined each environmental variable separately, showed that mean temperature and altitude were significantly correlated with all family- and species-level assemblages, while PCO1 from the vegetation analyses was significantly correlated with both family-level assemblages, but only the December ichneumonid assemblage, and the February diapriid assemblage (Table 4). Only mean temperature or altitude, however, was selected as the explanatory variable in each sequential test. Despite being significant in several of the marginal tests, PCO1 was not included in sequential models as it was highly correlated ($r > 0.9$) with mean temperature and altitude, and explained either slightly less or the same proportion of variation as temperature or altitude alone (Table 4).

DISCUSSION

This study has shown that the assemblage composition of parasitic Hymenoptera changes significantly across altitude both at the family level and at the morphospecies level within two diverse, large families. We found, however, gradual rather than blocked altitudinal turnover with a clear separation only between lowland (300 and 500 m asl) and upland (900 and 1100 m asl) assemblages, rather than the distinct assemblages at each altitude seen in other insect taxa examined in the adjacent IBISCA-Queensland transect (ants, moths and beetles: summarised in Kitching *et al.* 2013). Keeping in mind that our study used the same altitudes and experimental design, this contrast may reflect the higher trophic level and unique life history of parasitic Hymenoptera. Distributions of moths, for example, are likely to be determined by host plant availability, which is driven by abiotic conditions. Parasitoid assemblages may be affected by an additional suite of other factors such as the availability, density and assemblage composition of their hosts. Furthermore, the ants, moths and beetles from the IBISCA transect were identified to species level, suggesting that we may have found more distinct altitudinal assemblages if our parasitoids were identified to species level. However, similar patterns of distinct lowland and upland assemblages in rainforest have been found at the species level in dung beetles (Escobar *et al*. 2005), ants (Longino & Colwell 2011), spiders (Staunton *et al*. 2011) and insects with low dispersal ability (Yeates & Monteith 2008). These taxa also show some form of specialisation or occupy higher trophic levels, suggesting that life history, rather than taxonomic resolution, may have a greater influence on altitudinal patterns of assemblage composition.

Of the six families highly correlated with family-level assemblage patterns, only the Ichneumonidae, Braconidae and Diapriidae were correlated with both the December and February ordinations (Fig. 2a,b). Most of these families peaked in abundance at low and mid-altitude (300 and 500 m) in December and at high altitude in February. These seasonal differences in the altitudinal patterns of abundance of these parasitoid families may be due to their later emergence times at higher, cooler elevations. All poikilotherms show longer development times at lower temperatures (Speight *et al*. 1999), and several biological control studies have demonstrated this for hymenopteran parasitoids (Ables *et al*. 1976; Minkenberg 1989; Logan & Thomson 2002). In addition, some parasitoids that enter diapause at low temperatures are triggered by higher temperatures to break diapause and continue development (Hertlein 1986; Garcia *et al*. 2002). It is likely, therefore, that parasitoids at lower elevations, experiencing higher temperatures, develop faster and emerge earlier than those at higher elevations. We suggest that, as temperatures increase from spring into summer, populations at higher altitude peak in abundance, whereas populations at lower altitude decrease because of mortality following oviposition, consequently causing differences in altitudinal assemblage patterns between spring and summer (Hodkinson *et al*. 1999).

In concordance with the family-level analysis, both ichneumonid and diapriid assemblages analysed at the morphospecies level had significantly different lowland and upland assemblages. The diapriid ordinations showed some high-altitude clusters, with the two most abundant morphospecies driving this pattern. The ichneumonid ordination, however, showed no clear pattern and lacked any highly correlated morphospecies. Altitudinal studies in Costa Rica found that the Diapriidae were more diverse in high-altitude cloud forest compared with lower altitudes and that montane assemblages had mainly dipteran hosts (Hanson & Gauld 2000). Schizophoran flies in the Australian Wet Tropics exhibit a similar turnover in species with a distinct highland assemblage (Wilson *et al*. 2007), and a similar pattern was found at the family level for Diptera along the IBISCA-Queensland gradient (Lambkin *et al*. 2011). Rather than responding directly to environmental factors then, assemblage patterns of the Diapriidae may be more strongly reflecting the availability and composition of their predominantly dipteran hosts. The Ichneumonidae, on the other hand, while mainly having lepidopteran hosts, also parasitise a range of other insect taxa (Gauld 1984; Naumann 1991). As such, different subfamilies within the Ichneumonidae may be responding differently to changes in altitude and associated temperature regimes, resulting in the more dispersed pattern we observed. Hanson and Gauld (2000) reported that the ichneumonid subfamilies Ophioninae, Rhyssinae and Labeninae are more diverse in lowland rainforest of Costa Rica whereas Bachinae and Diplazontinae are more diverse in cloud forest. Further taxonomic analysis of the Ichneumonidae from this study will be needed to determine if these subfamilies show similar patterns along the Border Ranges gradient.

Mean temperature and, to a lesser extent, altitude were the variables that best explained the variation in both family and species-level assemblage composition in both December and February. The consistent selection of temperature or altitude as the best explanatory variables suggests that these are important factors driving parasitoid distributions. Strong relationships between temperature and assemblage composition have been found elsewhere in altitudinal studies of ants (Longino & Colwell 2011), pteridophytes (Kluge *et al*. 2006) and for springtails along the nearby IBISCA-Queensland gradient (Maunsell *et al*. 2013). These results should be interpreted with caution, however, as temperature and altitude may be acting as a proxy for tree species assemblages, which have also been found to be important in structuring parasitoid communities (Fraser *et al*. 2007; Arnan *et al*. 2011). Indeed, the primary PCO axis of tree species was highly correlated with parasitoid assemblages but was not selected in the final model because of its strong correlation with both temperature and altitude (Table 3). The lack of any significant relationship between parasitoid assemblage structure and the remaining environmental variables is perhaps surprising given that habitat complexity, tree cover and dead wood have been shown to affect parasitoid community composition significantly (Lassau & Hochuli 2005; Vanderwel *et al*. 2006; Arnan *et al*. 2011).

Our results show the potential of family-level analysis for identifying broad-scale patterns of parasitoid assemblage composition across environmental gradients. We show that for the parasitic Hymenoptera, family-level patterns of change with altitude were as strong as those indicated at the morphospecies level for two selected families. The changes in assemblage composition we have identified are important given the significant role of parasitoids in structuring food webs and, thereby, contributing to ecosystem functioning. Further studies will benefit from a more targeted approach, such as live rearing, which although time consuming will generate more detailed information on host records, species–species interactions and ecosystem measures such as rates of parasitism. Parasitic Hymenoptera represent a very diverse group of insects of considerable ecological importance worthy of much more study, not least at the community level.

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APPENDIX I

Identification code, latitude, longitude and environmental attributes of the 20 sites sampled for parasitic Hymenoptera. See Table 1 for explanation of environmental attributes

Site	Longitude (°E)	Latitude (°S)	Aspect	Slope (°)	Mean temperature (°C)	Litter depth (cm)	Canopy cover (%)	Dead wood (cm)	Altitude	Area (%)	Tree species richness
300 A	153° 01′ 12.1″	28° 24′ 35.1″	SW	10	15.62	1.85	84	54	303	5.02	14
300 B	153° 00′ 50.0″	28° 24′ 13.0′	NE	12	15.87	1.55	85.5	27	300	5.02	16
300 C	153° 01′ 14.0″	28° 24′ 21.1″	S SW	16	15.28	0.95	83.5	97	300	5.02	20
300 D	153° 01′ 16.4′	28° 24′ 15.3′	NW	8	15.57	1.3	83	120	327	5.02	26
500 A	153° 01′ 56.5″	28° 24′ 56.5″	S	26	15.15	0.65	84.5	111	500	8.34	12
500 B	153° 01′ 41.5″	28° 24′ 00.3″	W	15	15.23	0.75	73	59	500	8.34	14
500 C	153° 01′ 50.0″	28° 24′ 42.8″	NW	15	14.84	1.7	75.5	140	480	8.34	20
500 D	153° 01′ 49.5′	28° 24′ 36.2′	W SW	20	14.41	1.15	82.5	0	457	8.34	19
700 A	153° 02′ 59.5″	28° 23′ 58.7″	N	22	13.5	1.8	88.5	124	701	16.3	18
700 B	153° 02′ 53.7′	28° 23′ 42.0′	W	25	13.13	1	82.5	49	720	16.3	25
700 C	153° 02′ 34.8″	28° 23′ 50.6″	S SW	19	13.33	1.3	89.5	41	700	16.3	17
700 D	153° 02′ 24.1″	28° 24′ 00.1″	S SE	24	13.72	0.8	83	55	700	16.3	25
900 A	153° 04′ 01.2″	28° 23′ 18.1″	S SW	12	12.44	0.95	83.5	87	872	18.77	27
900 B	153° 04′ 19.5″	28° 23′ 18.1″	S	20	12.54	1.65	89	61	920	18.77	28
900 C	153° 04′ 39.6″	28° 23′ 16.5″	SW	24	12.64	1	78.5	92	900	18.77	27
900 D	153° 04′ 54.2′	28° 23′ 14.1′	SW	29	12.53	0.9	85	138	930	18.77	17
1100 A	153° 05′ 45.7″	28° 22′ 32.1″	N	9	12.1	1.95	86.5	31	1040	2.69	15
1100 B	153° 06′ 07.3″	28° 22′ 38.9″	SW	11	11.89	1.6	88	69	1040	2.69	19
1100 C	153° 06′ 22.4″	28° 22′ 39.7″	SE	7	11.83	1.95	72	71	1060	2.69	14
1100 D	153° 06′ 33.3′	28° 22′ 43.4′	SE	11	12.09	1.45	77	23	1060	2.69	19

APPENDIX II

Abundances of parasitic Hymenoptera families collected from Malaise traps (four per altitude) across five elevations (300, 500, 700, 900 and 1100 m asl) on two occasions (December 2010 and February 2011)

Family	December					February					Total
	300	500	700	900	1100	300	500	700	900	1100	
Ceraphronoidea											
Ceraphronidae	1	5	4	8	4	1	5	3	3	8	42
Megaspilidae	8	6	6	2	2	1	2	4	5	13	49
Evanioidea											
Evaniidae	4	1	1	0	0	1	1	0	0	0	8
Gasteruptiidae	0	0	0	0	0	0	0	2	10	0	12
Ichneumonoidea											
Ichneumonidae	92	59	105	17	12	58	69	68	69	43	592
Braconidae	204	225	167	108	27	45	143	121	192	135	1367
Proctotrupoidea											
Diapriidae	271	252	623	331	379	47	145	287	520	906	3761
Proctotrupidae	2	1	0	1	0	0	0	1	2	1	8
Scelionoidea											
Platygasteridae	97	73	125	82	17	28	62	116	134	145	879
Scelionidae	148	110	56	52	34	35	89	67	151	232	974
Cynipoidea											
Figitidae	61	42	13	3	1	17	43	15	30	20	245
Chalcidoidea											
Chalcididae	1	0	0	0	0	0	0	0	0	0	1
Eurytomidae	0	1	0	0	1	1	0	0	0	0	3
Agaonidae	0	0	0	0	0	0	2	0	0	0	2
Pteromalidae	9	16	16	7	5	3	12	12	29	64	173
Eucharitidae	1	0	15	0	0	0	1	1	0	13	31
Eupelmidae	0	0	2	4	0	0	0	1	2	0	9
Encrytidae	7	3	1	9	0	7	4	6	14	4	55
Aphelinidae	1	0	0	0	0	0	0	0	3	0	4
Eulophidae	30	45	42	21	3	15	35	53	21	7	272
Myrmaridae	20	26	13	4	8	11	20	10	10	31	153
Total	957	865	1189	649	493	270	633	767	1195	1622	8640

APPENDIX III

Abundances of Ichneumonidae and Diapriidae morphospecies collected from Malaise traps (four per altitude) across five altitudes (300, 500, 700, 900 and 1100 m asl) on two occasions (December 2010 and February 2011).

Morphospecies	December					300	February				Total
	300	500	700	900	1100		500	700	900	1100	
Ichneumonidae 1	11	0	1	0	0	16	3	1	0	0	32
Ichneumonidae 2	5	5	3	1	0	2	4	5	15	6	46
Ichneumonidae 3	1	0	0	0	0	0	0	0	0	0	1
Ichneumonidae 4	4	0	0	0	0	0	2	0	0	0	6
Ichneumonidae 5	4	1	7	1	1	0	0	0	0	1	15
Ichneumonidae 7	3	0	1	0	0	1	0	2	1	0	8
Ichneumonidae 8	1	0	0	0	0	0	0	0	0	0	1
Ichneumonidae 9	2	0	4	1	0	0	0	3	4	1	15
Ichneumonidae 10	2	1	1	0	0	2	0	0	0	0	6
Ichneumonidae 11	0	0	4	2	0	0	0	0	0	0	6
Ichneumonidae 12	0	0	0	1	1	0	0	2	2	0	6
Ichneumonidae 13	5	0	0	0	0	0	0	0	0	0	5
Ichneumonidae 14	5	2	2	1	3	1	2	0	1	0	17
Ichneumonidae 15	13	15	47	2	0	3	11	31	25	7	154
Ichneumonidae 16	4	2	10	0	0	1	0	3	2	0	22
Ichneumonidae 17	1	0	0	0	0	1	0	0	0	0	2
Ichneumonidae 20	0	0	1	0	2	0	0	0	0	4	7
Ichneumonidae 21	0	0	0	0	0	0	0	0	1	6	7
Ichneumonidae 22	1	0	0	0	0	0	0	0	0	0	1
Ichneumonidae 23	1	1	0	1	1	2	1	0	0	0	7
Ichneumonidae 24	1	0	0	0	0	0	0	0	0	0	1
Ichneumonidae 26	0	1	0	0	0	0	0	0	0	0	1
Ichneumonidae 27	1	0	1	0	0	1	0	0	1	0	4
Ichneumonidae 28	19	22	5	0	1	10	34	6	8	8	113
Ichneumonidae 29	1	0	0	0	0	0	0	0	0	0	1
Ichneumonidae 30	1	0	0	0	0	0	0	0	0	0	1
Ichneumonidae 31	0	0	0	0	0	0	0	5	0	0	5
Ichneumonidae 32	1	0	0	0	0	2	2	0	0	0	5
Ichneumonidae 33	0	0	0	0	0	0	0	0	0	1	1
Ichneumonidae 34	1	0	0	0	0	0	0	0	0	0	1
Ichneumonidae 35	2	0	0	0	0	0	0	1	0	0	3
Ichneumonidae 36	1	0	0	0	0	0	0	0	0	0	1
Ichneumonidae 37	1	2	0	0	0	0	0	0	0	0	3
Ichneumonidae 38	0	1	0	0	0	0	1	0	0	0	2
Ichneumonidae 39	0	1	1	0	1	0	0	1	0	0	4
Ichneumonidae 40	0	2	1	2	0	0	0	0	0	4	9
Ichneumonidae 42	0	2	0	0	0	0	0	0	0	0	2
Ichneumonidae 43	0	1	0	2	0	0	0	1	0	0	4
Ichneumonidae 44	0	1	0	0	0	0	0	0	0	0	1
Ichneumonidae 46	0	0	8	0	0	0	0	0	0	0	8
Ichneumonidae 47	0	0	2	1	3	0	0	0	0	1	7
Ichneumonidae 50	0	0	1	0	0	0	0	0	0	0	1
Ichneumonidae 51	0	0	1	0	0	0	0	0	0	0	1
Ichneumonidae 52	0	0	1	1	0	0	0	0	1	0	3
Ichneumonidae 53	0	0	0	1	0	0	1	1	0	0	3
Ichneumonidae 60	0	0	0	0	0	2	0	0	0	0	2
Ichneumonidae 61	0	0	0	0	0	2	0	0	0	0	2
Ichneumonidae 62	0	0	0	0	0	3	0	0	1	0	4
Ichneumonidae 63	0	0	0	0	0	1	0	0	0	0	1
Ichneumonidae 64	0	0	0	0	0	1	0	0	0	0	1
Ichneumonidae 65	0	0	0	0	0	1	0	0	0	0	1
Ichneumonidae 66	0	0	0	0	0	1	0	2	0	0	3
Ichneumonidae 67	0	0	0	0	0	0	1	0	0	0	1
Ichneumonidae 68	0	0	0	0	0	0	1	0	0	0	1
Ichneumonidae 69	0	0	0	0	0	0	1	0	0	0	1
Ichneumonidae 70	0	0	0	0	0	0	1	0	0	0	1
Ichneumonidae 71	0	0	0	0	0	0	1	0	0	0	1
Ichneumonidae 72	0	0	0	0	0	0	0	2	1	0	3

Appendix III *Continued*

Morphospecies	December					300	February				Total
	300	500	700	900	1100		500	700	900	1100	
Ichneumonidae 73	0	0	0	0	0	0	0	0	2	0	2
Ichneumonidae 74	0	0	0	0	0	0	0	0	1	0	1
Ichneumonidae 76	0	0	0	0	0	3	0	0	0	0	3
Ichneumonidae 77	0	0	0	0	0	0	1	0	0	0	1
Ichneumonidae 78	0	0	0	0	0	0	2	1	0	0	3
Ichneumonidae 79	0	0	0	0	0	0	0	1	0	0	1
Ichneumonidae 80	0	0	0	0	0	0	0	0	1	0	1
Ichneumonidae 81	0	0	0	0	0	0	0	0	1	0	1
Ichneumonidae 82	0	0	0	0	0	0	0	0	1	0	1
Ichneumonidae 83	0	0	0	0	0	0	0	0	0	1	1
Ichneumonidae 84	0	0	0	0	0	0	0	0	0	1	1
Ichneumonidae 85	0	0	0	0	0	0	0	0	0	1	1
Ichneumonidae 86	0	0	0	0	0	0	0	0	0	1	1
Diapriidae 1	2	0	0	1	0	0	0	0	3	0	6
Diapriidae 2	19	6	26	3	23	1	3	4	14	21	120
Diapriidae 3	2	1	2	3	1	0	1	1	0	1	12
Diapriidae 4	5	8	5	1	0	5	11	1	46	4	86
Diapriidae 5	1	1	0	1	0	0	0	0	0	1	4
Diapriidae 6	1	0	0	0	0	0	0	0	2	0	3
Diapriidae 7	3	9	0	2	0	1	11	1	2	0	29
Diapriidae 8	3	3	15	0	0	0	1	0	0	2	24
Diapriidae 9	1	2	7	0	6	1	0	2	12	24	55
Diapriidae 10	9	6	8	6	2	0	2	0	0	1	34
Diapriidae 11	6	1	11	2	1	1	3	1	10	47	83
Diapriidae 12	5	2	1	2	4	1	1	4	0	5	25
Diapriidae 13	15	6	7	1	0	1	11	4	0	1	46
Diapriidae 14	86	74	236	102	88	11	22	70	167	413	1269
Diapriidae 15	21	27	90	16	33	4	11	31	48	51	332
Diapriidae 16	2	8	10	7	0	0	10	17	10	23	87
Diapriidae 17	24	26	50	38	48	5	11	4	21	40	267
Diapriidae 18	3	0	0	0	0	0	0	0	0	0	3
Diapriidae 19	12	19	17	9	0	0	0	11	14	43	125
Diapriidae 20	1	0	0	0	0	0	0	0	0	0	1
Diapriidae 21	2	0	0	0	0	0	0	0	0	0	2
Diapriidae 22	1	6	1	4	2	0	1	2	0	2	19
Diapriidae 23	7	3	1	22	49	0	0	3	28	43	156
Diapriidae 24	7	1	14	3	25	1	7	0	2	3	63
Diapriidae 25	12	13	30	42	35	1	8	55	41	70	307
Diapriidae 26	3	3	6	1	0	3	11	20	21	20	88
Diapriidae 27	1	0	0	2	0	0	0	0	0	0	3
Diapriidae 28	2	8	27	15	21	0	2	6	12	15	108
Diapriidae 30	2	1	0	9	6	0	2	1	4	8	33
Diapriidae 31	0	0	1	1	0	0	0	4	0	0	6
Diapriidae 32	1	2	1	0	0	2	1	3	22	12	44
Diapriidae 33	1	0	0	0	0	0	0	0	1	0	2
Diapriidae 34	0	0	0	1	0	0	0	0	2	0	3
Diapriidae 35	2	1	7	7	2	2	7	4	2	5	39
Diapriidae 36	2	0	3	0	0	3	0	16	15	7	46
Diapriidae 37	3	1	3	7	5	0	2	4	6	18	49
Diapriidae 38	1	4	4	7	2	0	1	2	0	6	27
Diapriidae 39	0	1	5	0	11	0	0	0	0	5	22
Diapriidae 40	0	1	0	1	12	0	0	0	0	0	14
Diapriidae 41	2	3	2	2	0	0	2	0	2	5	18
Diapriidae 42	0	2	0	0	0	0	0	0	0	0	2
Diapriidae 43	0	0	0	1	0	0	0	0	0	0	1
Diapriidae 44	0	1	1	0	0	4	0	0	0	0	6
Diapriidae 45	0	1	0	0	0	0	0	0	0	2	3
Diapriidae 46	0	0	1	0	0	0	0	0	0	0	1
Diapriidae 47	0	0	8	0	0	0	0	0	0	0	8
Diapriidae 48	0	0	11	6	0	0	0	6	7	7	37
Diapriidae 49	0	0	8	0	0	0	0	0	0	2	10
Diapriidae 50	0	0	1	2	0	0	0	1	0	0	4
Diapriidae 51	0	0	0	3	0	0	0	0	3	0	6

Appendix III *Continued*

Morphospecies	December					300	February				Total
	300	500	700	900	1100		500	700	900	1100	
Diapriidae 52	0	0	0	1	4	0	0	0	0	6	11
Diapriidae 54	0	1	7	0	0	0	1	1	0	0	10
Diapriidae 55	0	0	0	1	0	0	0	6	0	6	13
Diapriidae 56	0	0	0	0	1	0	0	0	0	1	2
Diapriidae 57	0	0	0	0	2	0	0	0	2	4	8
Diapriidae 58	0	0	0	0	0	0	0	0	1	0	1