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The IBISCA-Queensland Project

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Altitudinal and seasonal variation in the family-level assemblages of flies (Diptera) in an Australian subtropical rainforest: one hundred thousand and counting!

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ABSTRACT

Many surveys around the world have examined the altitudinal or seasonal variation of invertebrate biodiversity but few have concentrated on the fly fauna because of difficulties with the amount of material and identification. We examined family-level assemblages of flies collected in Malaise traps from rainforest at Lamington National Park, south-east Queensland across altitude and seasons. We found significant effects of both season and altitude on the overall abundance of other Diptera (without lower Diptera), with a significant interaction effect so that abundances in summer were much higher than those in winter, but only at mid to high altitudes. We also found significant effects of both season and altitude on the family richness of other Diptera, and again the interaction of these factors was significant. A clear seasonal influence was noted at mid to high elevations with a progressive decline in the number of fly families captured from summer to Spring to winter together with a decline with increasing altitude, at least in Spring and winter. Within each altitude, all seasonal fly assemblages were significantly different, with the exception of those from summer and autumn at 500 m a.s.l. However, the altitudinal responses of fly assemblages were less strong and not consistent between seasons. Six families were most strongly correlated with these patterns; Asilidae,

Chloropidae, Dolichopodidae, Empididae, Muscidae and Phoridae. Asilidae, Dolichopodidae and Empididae declined in abundance with increasing altitude. Only Chloropidae and Muscidae appeared to increase in abundance with altitude, at least between 700 and 1100 m but only in summer. Dolichopodids and muscids progressively declined in abundance as the sampling period became cooler, while asilids were captured throughout the transect in summer, were collected from only the two lowest elevations in Spring, and were completely absent in winter. All families had a limited presence at higher altitudes during July, the coldest and driest month. The Empididae, Phoridae, Chloropidae, and Drosophilidae appear to be able to survive at lower altitudes in winter, and become more abundant at higher cooler altitudes in summer. Generalist behaviours, lack of host specificity, larvae within the protected soil or leaf litter habitat, and ability as adults to fly considerable distances may provide many fly families with the capacity to cope with climate change, as they have in the past. □ *Diptera, altitude, seasonality, IBISCA-Queensland, Malaise traps.*

Studies of altitudinal gradients offer an ideal opportunity to study natural variability of plant and animal populations across a range of climatic conditions. Consequently, these studies may offer a tool for predicting responses of these organisms to changes in climate. Invertebrates represent a huge proportion of rainforest biodiversity and are considered vital for ecosystem function. The distribution of many invertebrate groups along altitudinal gradients, however, is poorly known, largely because of the massive diversity of invertebrates (see review in Novotny & Basset 2000) and most altitudinal studies have focussed on a subset of animals. Commonly studied groups include beetles (Coleoptera) (Erwin 1982; Escobar *et al.* 2005; Monteith & Davies 1991), moths and butterflies (Lepidoptera) (Brehm *et al.* 2007; Brehm & Fiedler 2003; Fleishman *et al.* 2000; Wilson *et al.* 2007b), ants (Hymenoptera, Formicidae) (Botes *et al.* 2006; Bruhl *et al.* 1999; Fisher 1996, 1999; Sanders *et al.* 2007), and spiders (Araneae) (Chatzaki *et al.* 2005; Monteith & Davies 1991). Few studies have considered the turnover of fly (Diptera) species along an altitudinal gradient (McKie *et al.* 2005; Wilson *et al.* 2007a; Yeates 1985). Yet the Diptera offer a potentially useful study group in ecological surveys encompassing a wide range of anatomical and biological specialisations (Yeates *et al.* 2009) and probably the widest range of ecological roles of the four mega-diverse insect orders (Kitching *et al.* 2004, 2005). In addition they can be systematically sampled

with ease and represent a manageable number of families for identification (159 families, Yeates *et al.* 2009) making them a useful group to understand not only species turnover with altitude and therefore climate shifts, but also changes in ecosystem function along these natural gradients.

Direct altitudinal impacts on insects include changes to wing morphology associated with reduced flight activity, colour polymorphism to adjust body temperature at different altitudes, and variations in body size, phenology and fecundity (Hodkinson 2005). Additionally, changes in insect abundance and community composition might be expected in response to changes in environmental conditions associated with increasing altitude. However clear linear relationships are rarely found, for example, increases and decreases in species richness with increasing altitude, as well as mid-altitude peaks, have been reported previously (see review in Hodkinson 2005). Evidence of species turnover of flies with increasing altitude has been found in a number of studies (McKie *et al.* 2005; Wilson *et al.* 2007a; Yeates 1985). A survey of aquatic midges (Chironomidae) along altitudinal and latitudinal gradients found cool-adapted Gondwanan chironomids were more abundant at higher altitudes (McKie *et al.* 2005). In the case of schizophoran flies in the Australian Wet Tropics, Wilson *et al.* (2007a) determined that some morphospecies were found only at the upper limits of the studied altitudinal gradients. Furthermore, an increased dominance

of flies visiting flowers at higher altitudes was attributed to their ability to use lengthy sun basking, rather than relying on endothermally generated energy, to provide a competitive advantage in higher, colder altitudes (Arroyo *et al.* 1982; Kearns 1992; Warren *et al.* 1988).

Fly abundance and diversity can also be expected to vary in relation to season. For example, a 15 month survey of stiletto flies (Therevidae) in the Brisbane region demonstrated biannual peaks in abundance in Spring and autumn (Power 1998). Wilson *et al.* (2007a) demonstrated that the season of peak abundance for schizophoran flies changed with altitude in the Wet Tropics of Australia.

The IBISCA-Queensland Project (Kitching *et al.* 2011) was designed to document the current distributions of a wide range of invertebrate taxa along an altitudinal gradient within continuous subtropical rainforest in Lamington National Park, southeast Queensland. The aim was to identify taxa or suites of taxa that could be incorporated into long-term monitoring programmes to detect the impacts of climate change. This was achieved by employing a variety of sampling methods to collect invertebrates from a wide range of microhabitats. The aims of this study were to examine the altitudinal change in fly assemblages and to determine if this varied seasonally within subtropical rainforest at Lamington National Park, southeast Queensland.

METHODS

Study site

Sampling was conducted along the IBISCA-Queensland transect established within continuous subtropical rainforest in Lamington National Park at latitude 28°S. The transect ranged from 250 to 1140 m above sea level (a.s.l.) with four plots established at each of five altitudinal categories; 300, 500, 700, 900 and 1100 m a.s.l., giving a total of 20 plots. A description of the project aims is provided in Kitching *et*

al. (2011), and Laidlaw *et al.* (2011) provide a description of the associated vegetation.

Malaise trapping

To give a true indication of groups present at a site during a faunal survey, it is desirable to employ a collecting method that is unbiased and operates continually. The most effective means of obtaining specimens, and temporal and geographic distributional data, is the use of passive collecting methods (Darling & Packer 1988; Evans & Owen 1965). Malaise traps are a passive, unbiased, flight intercept sampling method that collects insects as they move through the air. The Malaise trap, first described by René Malaise (1937), is a bilateral trap; essentially an open-sided tent with entrances from both sides and an angled roof leading up to an apex where a collection chamber attaches to a removable collecting jar in which insects are killed and preserved (Southwood 1978). Townes (1972) found that a bicoloured trap (i.e. a combination of light flaps and a dark intercepting baffle) increased the catch by 70% (in shade) to 180% (in sunlight) compared to an all white trap. As Malaise traps may be left unattended for several days, they are useful for the study of insect fauna in areas that are difficult to access (Lambkin *et al.* 2002; Malaise 1937; Townes 1962, 1972) such as the dense rainforest in which this study was conducted. They sample fauna throughout the daily cycle and in all weather. The chief difficulty is finding a suitable location for the Malaise traps as they sample insects moving through a relatively small landscape. Where possible, we placed Malaise traps perpendicularly across observed flight paths, across gullies, or in sunlit clearings.

A single Malaise trap was operated for 10 days at each of the four plots located at each of the five altitudes (total of 20 traps) during October 2006 and January and July 2007. Half the Malaise traps used were a standard Townes design (Townes 1962, 1972) and obtained from Australian Entomological Supplies, New South Wales. The remaining traps were modified

Townes traps with curved roof panels designed by Michael Sharkey and manufactured by Sante Traps, Kentucky. Although we used Malaise traps of two slightly different designs we consider they had similar performance. All Malaise traps used were made of very fine mesh, were 2 m high at the head, with central panel about 2 m long, and had a white roof, and black walls and central barrier. The head, four corners, and tail of the roof were tied by ropes to vegetation and the base pegged to open the trap to its maximum width. The collecting jars were filled with at least 300 ml of 95% ethanol. Generally all four Malaise traps at a particular altitude were erected on the same day. In 2006 all traps were installed from 5-9 October and cleared from 15-19 October. In January 2007 traps were installed between the 13th and 16th and cleared between the 23rd and 26th. In July 2007 traps were installed between the 15th and 18th and cleared between the 25th and 28th.

Sorting

All Diptera were extracted from samples and sorted into lower Diptera (previously the Suborder Nematocera), lower Brachycera (previously Orthorrhapha and Cyclorrhapha Ashiza) and Schizophora. Specimens of lower Diptera within each sample were counted but not further identified. All specimens of lower Brachycera and Schizophora (collectively the Brachycera) in samples were sorted to family level and counted. Brachyceran families were identified using interactive Lucid 'On the Fly' keys (Hamilton *et al.* 2006) and a self-generated photographic guide to representatives of every brachyceran family found during the study (Figs 1-2).

Analyses

Lower Diptera were not sorted to family level but this group potentially comprised 23 families. Due to ubiquity and overwhelming abundance of lower Diptera along the transect, and its taxonomic inconsistency with the rest of the family-

level data, we analysed the total abundance of this group separately and did not incorporate it within assemblage-level multivariate analyses.

We tested the influence of two main factors, season (Spring, summer and winter) and altitude (300, 500, 700, 900 and 1100 m a.s.l.), and their interaction, on various aspects of fly diversity using PERMANOVA (permutational multivariate analysis of variance) available from PRIMER 6 (Clarke & Gorley 2006) and PERMANOVA+ add-on software packages (Anderson *et al.* 2008). PERMANOVA executes multivariate ANOVA, using permutation methods, to calculate *P* values derived from pseudo-*F* statistics of the distance measures. Effects of altitude and season were incorporated in the analyses as fixed factors and separate analyses were conducted for univariate (e.g. total abundance) and multivariate (family assemblages) response variables. Although PERMANOVA is designed primarily for multivariate analysis, univariate analysis is possible using Euclidean distances which yield Fisher's traditional univariate *F* statistic (Anderson *et al.* 2008). Univariate response variables included the total abundance of lower Diptera, the total abundance of other Diptera (lower Brachycera and Schizophora) and the family richness of other Diptera (i.e. the number of families per sample). Total abundance data were natural log-transformed, $\ln(x+1)$, before analyses. Multivariate analyses were performed on Bray-Curtis distance measures between plots, based on the natural log-transformed abundances of fly families (lower Brachycera and Schizophora). Type III sums of squares were used to calculate pseudo-*F* statistics, and *P* values were obtained using 9999 permutations of residuals under a reduced model. Post-hoc pairwise tests were used to compare differences between pairs of individual treatments, using a multivariate version of the *t*-statistic and Monte Carlo asymptotic *P* values (which are not restricted by the number of unique permutations). We also used PRIMER 6 to generate non-metric multidimensional-scaling (NMDS) ordinations (Clarke 1993) based on Bray-Curtis similarity matrices of

Variation in assemblages of flies (Diptera)

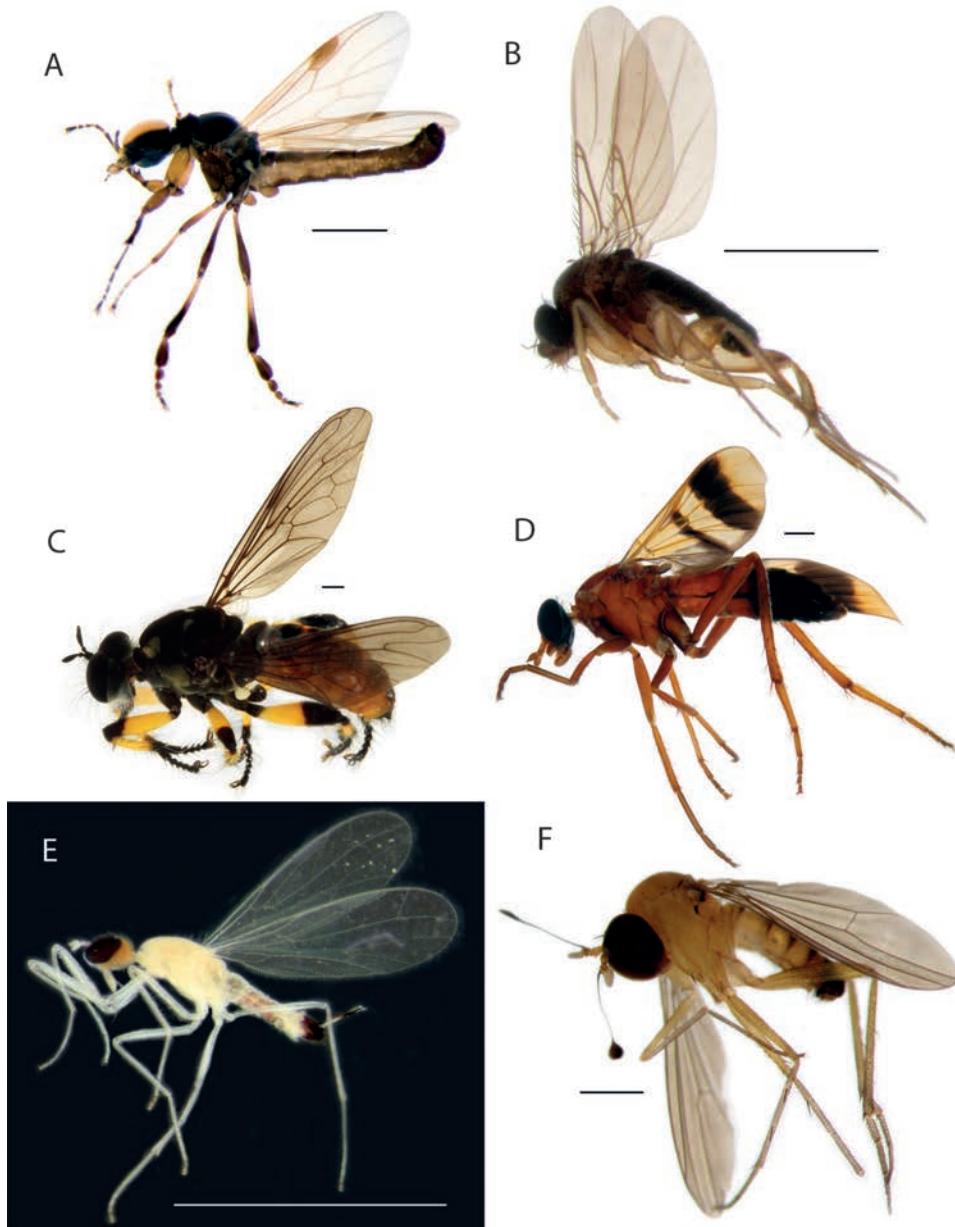


FIG. 1. Examples of fly families collected in IBISCA-Queensland in Malaise traps used in the easy visual guide for sorting prepared from photographs taken by N. Starick. A, *Dilophus* sp. Bibionidae, lower Diptera; B, Phoridae; C, *Laphria hirta* Ricardo, Asilidae; D, Undescribed genus and species of Therevidae; E, Hemerodromiinae, Empididae; F, *Yumbera callida* Parent, Dolichopodidae. Scale line = 1mm.

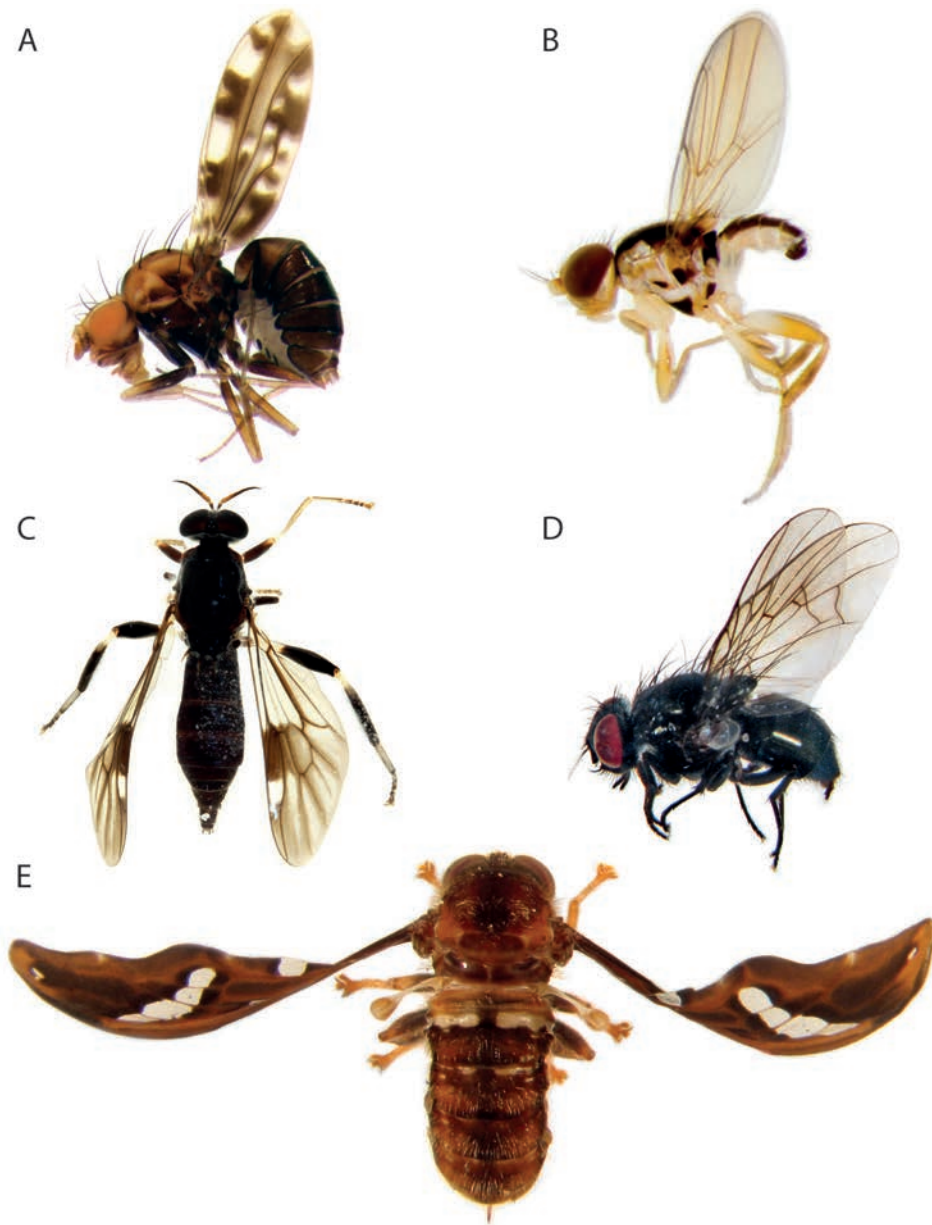


FIG. 2. Examples of fly families collected in IBISCA-Queensland in Malaise traps used in the easy visual guide for sorting prepared from photographs taken by N. Starick. A, *Tambourella endiandrae* Wheeler, Drosophilidae; B, Chloropidae; C, *Exaireta spinigera* (Wiedemann), Stratiomyidae; D, Muscidae; E, *Nycterimorpha speiseri* Lichtwardt, Nemestrinidae. Scale line = 1mm.

Variation in assemblages of flies (Diptera)

TABLE 1. Total numbers of individual Diptera in higher taxonomic groups and families collected at five altitudes (m above sea level) and during three seasons (October, January and July) using Malaise traps in Lamington National Park. Lower Diptera is 'Nematocera'.

Group	Family	300m	500m	700m	900m	1100m	Oct-06	Jan-07	Jul-07	Grand Total
Lower Diptera										
	Lower Diptera	17983	14954	19649	16532	13222	26173	41183	14984	82340
Orthorrhapha										
	Asilidae	53	12	18	6	4	14	79		93
	Bombyliidae	3		2				5		5
	Dolichopodidae	586	210	164	132	96	470	616	102	1188
	Empididae	545	329	241	280	84	629	730	120	1479
	Hybotidae	4		1	2		3	4		7
	Nemestrinidae		1					1		1
	Rhagionidae	8	14	6	5	8	35	6		41
	Stratiomyidae	184	61	87	51	7	168	211	11	390
	Tabanidae	2		1	5	1	1	8		9
	Therevidae	22	11	9	3		15	30		45
Cyclorrhapha Aschiza										
	Phoridae	4460	7036	3024	4050	1611	4704	7522	7955	20181
	Pipunculidae	18	10	6	1		12	22	1	35
	Platypezidae	8	7	10	15	2	5	37		42
	Sciadoceridae		1	1		2	2		2	4
	Syrphidae	31	2	6	3	3	6	39		45
Cylorrhapha Schizophora										
	Agromyzidae	4			1		1	2	2	5
	Anthomyidae	3					2		1	3
	Asteiidae	1						1		1
	Rhinophoridae		1		3			4		4
	Calliphoridae	8	4	7	67	120	14	192		206
	Chloropidae	177	333	138	172	149	281	465	223	969
	Clusiidae	12	13	9	13	17	19	30	15	64
	Cryptochaetidae	2						2		2
	Cypselosomatidae		2					2		2
	Drosophilidae	112	288	86	351	64	73	527	301	901
	Ephydriidae	2	4	3		7	10	3	3	16
	Heleomyzidae	54	47	29	39	29	85	47	66	198

TABLE 1 continued...

Group	Family	300m	500m	700m	900m	1100m	Oct-06	Jan-07	Jul-07	Grand Total
	Helosciomyzidae		1	4	1	124	36	89	5	130
	Lauxaniidae	28	34	29	43	54	81	54	53	188
	Lonchaeidae	3	2		1		4		2	6
	Micropezidae	13	2	6	1		9	13		22
	Milichiidae	4	8	2	7	4	20	5		25
	Muscidae	153	51	108	119	255	209	436	41	686
	Neriidae	4	1				4	1		5
	Neurochaetidae		3					2	1	3
	Platystomatidae	5	4			2		11		11
	Pyrgotidae			2				2		2
	Sarcophagidae	8	1	2			1	9	1	11
	Sepsidae	7	7	2		4	9	6	5	20
	Sphaeroceridae	273	159	58	103	158	396	200	155	751
	Tachinidae	88	19	44	63	37	29	217	5	251
	Tanypezidae	6	1	1			5	3		7
	Tephritidae	2	3	3	3	4	3	10	2	15
	Teratomyzidae	1	22	8	6	4	2	9	30	41
Total no. individuals		24877	23658	23766	22078	16072	33530	52835	24086	110451
Number of families		38	37	34	30	27	36	42	25	45

fly families calculated between each plot pair, with 100 random restarts.

Finally, a Bio-Env procedure (available from the BEST routine of PRIMER 6) was executed to find a subset of fly families that best 'explained' the overall pattern of whole (all families) fly assemblages. Bio-Env generates all possible combinations of the subset of fly families and compares their similarities to the whole fly assemblages using a selected rank correlation method (Clarke & Gorley 2006). We set the maximum number of fly families included in subsets to five and used Spearman rank correlation.

RESULTS

A total of 110451 fly specimens were collected across the three seasons and five altitudinal zones (Table 1). Lower Diptera dominated, comprising 74.5% of the total catch. The remaining flies (28111 specimens) were represented by 44 families, with most specimens from the family Phoridae (in the lower Brachycera); 20181 specimens representing 18.3% of the total fly specimens. Of the remaining 7930 specimens around 80% were comprised of seven families; Empididae (18.6%) (Fig. 1E), Dolichopodidae (14.9%) (Fig. 1F), Chloropidae (12.2%) (Fig. 2B), Drosophilidae (11.4%) (Fig. 2A), Sphaeroceridae (9.5%), Muscidae (8.7%) (Fig. 2D) and Stratiomyidae (4.9%) (Fig. 2C).

Variation in assemblages of flies (Diptera)

TABLE 2. Summary results of PERMANOVA tests, showing pseudo-*F* and *P* values of the two main factors, altitude and season, and their interaction. Four separate tests were conducted for three univariate response variables and fly assemblage data. Degrees of freedom for altitude, season, interaction and residual are 4, 2, 8 and 45 respectively. Lower Diptera is 'Nematocera' and other Diptera is 'lower Brachycera' + Schizophora.

	Altitude		Season		Interaction	
	Pseudo- <i>F</i>	<i>P</i>	Pseudo- <i>F</i>	<i>P</i>	Pseudo- <i>F</i>	<i>P</i>
Univariate analyses						
Abundance (lower Diptera)	0.535	0.713	9.431	<0.001	1.351	0.237
Abundance (other Diptera)	5.294	0.001	10.397	<0.001	5.695	<0.001
Family richness (other Diptera)	10.583	<0.001	70.992	<0.001	3.492	0.002
Multivariate						
Family assemblage (other Diptera)	4.594	<0.001	17.48	<0.001	3.081	<0.001

TABLE 3. Summary results of post-hoc tests comparing differences in fly family assemblages between pairs of seasons. Due to a significant interaction between altitude and season, separate post-hoc tests were executed for each of the five altitudinal zones. *P* values were calculated by 9999 Monte Carlo (MC) asymptotic permutations. Significant *P* values are shown in bold.

Groups	<i>P</i> (MC) values				
	300 m	500 m	700 m	900 m	1100 m
Oct, Jan	0.044	0.082	0.033	0.040	0.014
Oct, Jul	0.009	0.008	0.007	0.035	0.014
Jan, Jul	0.007	0.008	0.002	0.004	0.003

Fly abundance and family richness

The total abundance of flies (lower and other Diptera combined) declined considerably from summer to Spring to winter (52 835 to 33 530 to 24 086 specimens respectively) and gradually declined with increasing altitude (24 877 specimens at 300 m a.s.l. to 16 072 at 1100 m, see Table 1). The family richness of the other Diptera showed similar seasonal (41 families in summer, 36 in Spring and 24 in winter) and altitudinal (38 families at 300 a.s.l. declining to 26 at 1100 m a.s.l., see Table 1) patterns.

TABLE 4. Summary results of post-hoc tests comparing differences in fly family assemblages between pairs of altitudes. Due to a significant interaction between altitude and season, separate post-hoc tests were executed for each of the three seasons. *P* values were calculated by 9999 Monte Carlo (MC) asymptotic permutations. Significant *P* values are shown in bold.

Groups	<i>P</i> (MC) values		
	October (spring)	January (summer)	July (winter)
300m, 500m	0.019	0.122	0.033
300m, 700m	0.012	0.280	0.038
300m, 900m	0.010	0.058	0.043
300m, 1100m	0.003	0.008	0.021
500m, 700m	0.135	0.432	0.006
500m, 900m	0.241	0.212	0.013
500m, 1100m	0.017	0.033	0.004
700m, 900m	0.305	0.588	0.257
700m, 1100m	0.013	0.020	0.092
900m, 1100m	0.127	0.091	0.194

We found no significant effect of altitude on the abundance of lower Diptera (Table 2) which occurred in high numbers across all elevations (Fig. 3A). However, we did find a significant

effect of season (Table 2), with post-hoc pair-wise comparisons showing significantly fewer lower Diptera collected in July (Fig. 3A). In contrast, we found significant effects of both season and altitude on the overall abundance of other Diptera, but we also found a significant interaction effect (Table 2). There appeared to be a strong seasonal influence, with abundances in January much higher than those in July, but only at mid to high altitudes (700-1100 m) (Fig. 3B). It was difficult to discern any meaningful influence of altitude on the abundance of other Diptera as seasonal responses were highly idiosyncratic (Fig. 3B). Similarly, we found significant effects of both season and altitude on the family richness of other Diptera, and again the interaction of these factors was significant (Table 2). As with the abundance, there appeared to be a clear seasonal influence at mid to high elevations with a progressive decline in the number of fly families captured from January to October to July (Fig. 3C). There also appeared to be a trend for the number of fly families to decline with increasing altitude, at least in October and July (Fig. 3C).

Fly family-level assemblages

Initially we looked for patterns in family-level fly assemblages using NMDS ordination, incorporating samples from all seasons and altitudes (based on natural log-transformed abundances of fly families excluding lower Diptera). There appeared to be a seasonal pattern with samples collected in January (summer) and July (winter) clearly separated, whereas those from October (Spring) were intermediate (Fig. 4A). In contrast, the effect of altitude was much less apparent in the ordination (Fig. 4B).

Although we found significant effects of both season and altitude on family-level assemblages, we also found a significant interaction between these main factors (Table 2). Consequently post-hoc analyses involved investigation of fly assemblages between seasons within each of the

five altitudes, and investigation of fly assemblages between altitudes within each of the three seasons.

Within each altitude, all seasonal fly assemblages were significantly different, with the exception of those from October and January at 500 m a.s.l. (Table 3). However, the altitudinal responses of fly assemblages were less strong and not consistent between seasons. In October, assemblages at the lowest (300 m) and highest (1100 m) altitudes were distinct, although there was no significant difference between those at 1100 and 900 m (Table 4). In January only assemblages from the highest elevation were significantly different, but again not from those at 900 m (Table 4). In stark contrast, July assemblages from the two lowest elevations (300 and 500 m) were significantly different from those at higher elevations, and from each other (Table 4). These results are supported by the NMDS ordinations which in October and January have the 300 and 1100 m assemblages widely separated with those of intermediate altitudes scattered between (Fig. 5A, B). The pattern in July was idiosyncratic with the samples from 300 and 500 m having distinct assemblages, whereas there were no apparent patterns among the other altitudes (Fig. 5C).

The Bio-Env procedure selected subsets of five fly families that were highly correlated with the pattern of fly assemblages based on all families. Only six families were included in the three most strongly correlated subsets (correlation coefficient 0.890-0.892); Asilidae, Chloropidae, Dolichopodidae, Empididae, Muscidae and Phoridae. Examining the individual abundances of these families across altitude in each sampling period, no consistent trend was apparent (Fig. 6). Three families (Asilidae, Dolichopodidae and Empididae) declined in abundance with increasing altitude (Fig. 6A, C, D). Only the Chloropidae (Fig. 6B) and Muscidae (Fig. 6E) appeared to increase in abundance with altitude, at least between 700 and 1100 m a.s.l., but only in the summer (January) sampling period. Some fly families showed clear seasonal signals. Dolichopodids and muscids

Variation in assemblages of flies (Diptera)

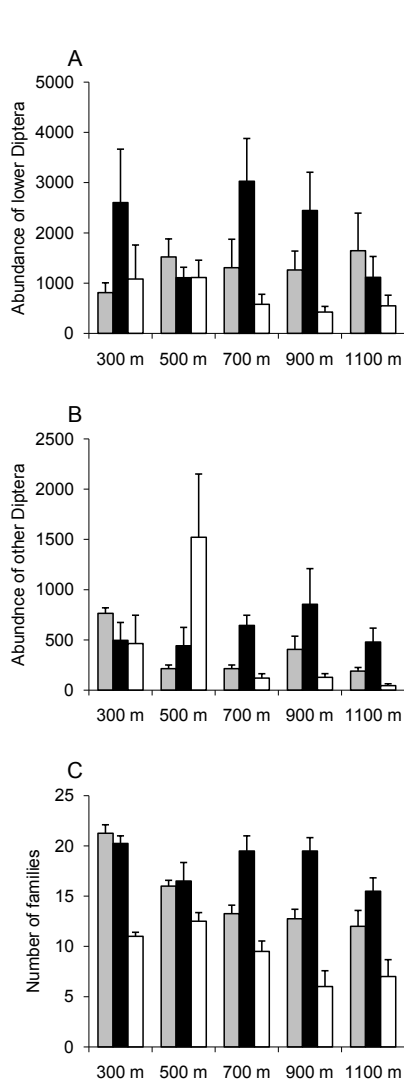


FIG. 3. Mean (+SE) values of A, total abundance of lower Diptera (= 'Nematocera'); B, total abundance of other Diptera (= 'lower Brachycera' and Schizophora), and; C, total number of fly families across five altitudes and three seasons, spring (October) shaded bars, summer (January) solid bars and winter (July) open bars.

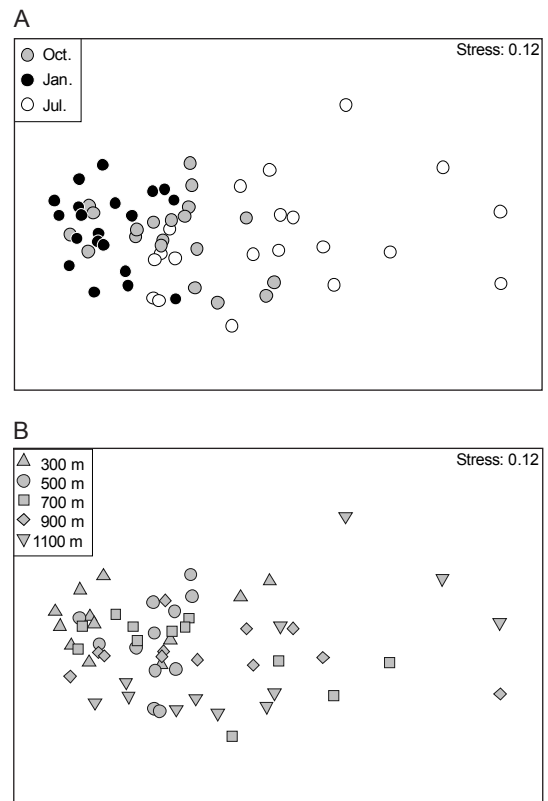


FIG. 4. NMDS ordinations of family-level fly assemblages based on log-transformed abundances (excluding lower Diptera). The same ordination was generated twice to visually present; A, seasonal and; B, altitudinal variations in assemblage composition.

progressively declined in abundance as the sampling period became cooler (Fig. 6C, E), while asilids were captured throughout the transect in summer, were collected from only the two lowest elevations in Spring, and were completely absent in winter (Fig. 6A). All families had a limited presence at higher altitudes during July, the coldest and driest month.

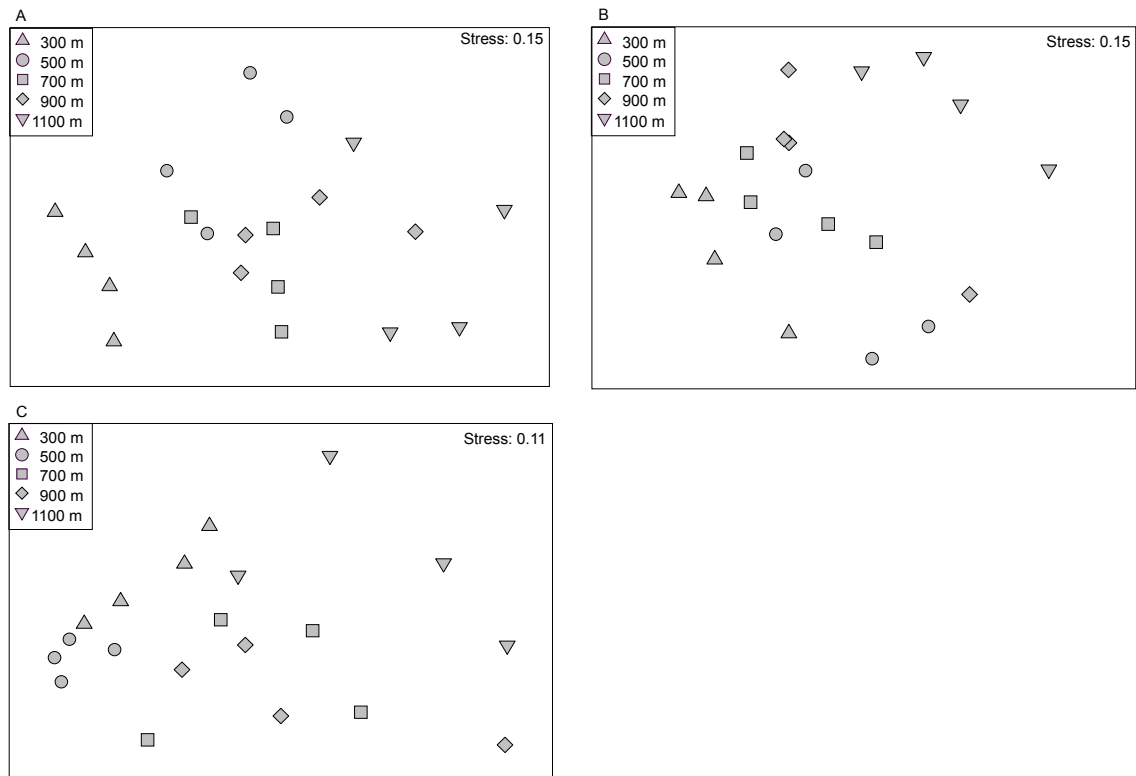


FIG. 5. NMDS ordinations of family-level fly assemblages based on log-transformed abundances (excluding lower Diptera). Three separate ordinations were generated for fly assemblages collected in A, October; B, January and; C, July.

DISCUSSION

The present study demonstrates the overwhelming presence of flies along the altitudinal gradient and across all sampling periods. It also demonstrates the complex response of different fly groups to environmental factors associated with both season and changes in altitude. A significant part of the fly fauna were those flies that made up the lower Diptera. Although further sorting is required to determine an assemblage response to changes in altitude and season, it was clear that the lower Diptera are a conspicuous part of the insect fauna at all altitudes, whose numbers diminish in cooler, drier seasons.

The remaining flies, the lower Brachycera and Schizophora (other Diptera), did show changes in overall abundance and family richness, as well as different community assemblages among altitudes. Overwhelmingly, however, this response was modified by a strong seasonal influence, with altitudinal patterns differing between seasons. Identifying a clear, altitudinal “gradient” response is difficult and the lack of clear result is likely to reflect several factors: 1) the divergent environmental requirements of both immature and adult flies, with the unique responses of individual families contributing to the lack of pattern, 2) the coarse taxonomic level at which this analysis was undertaken (i.e. family)

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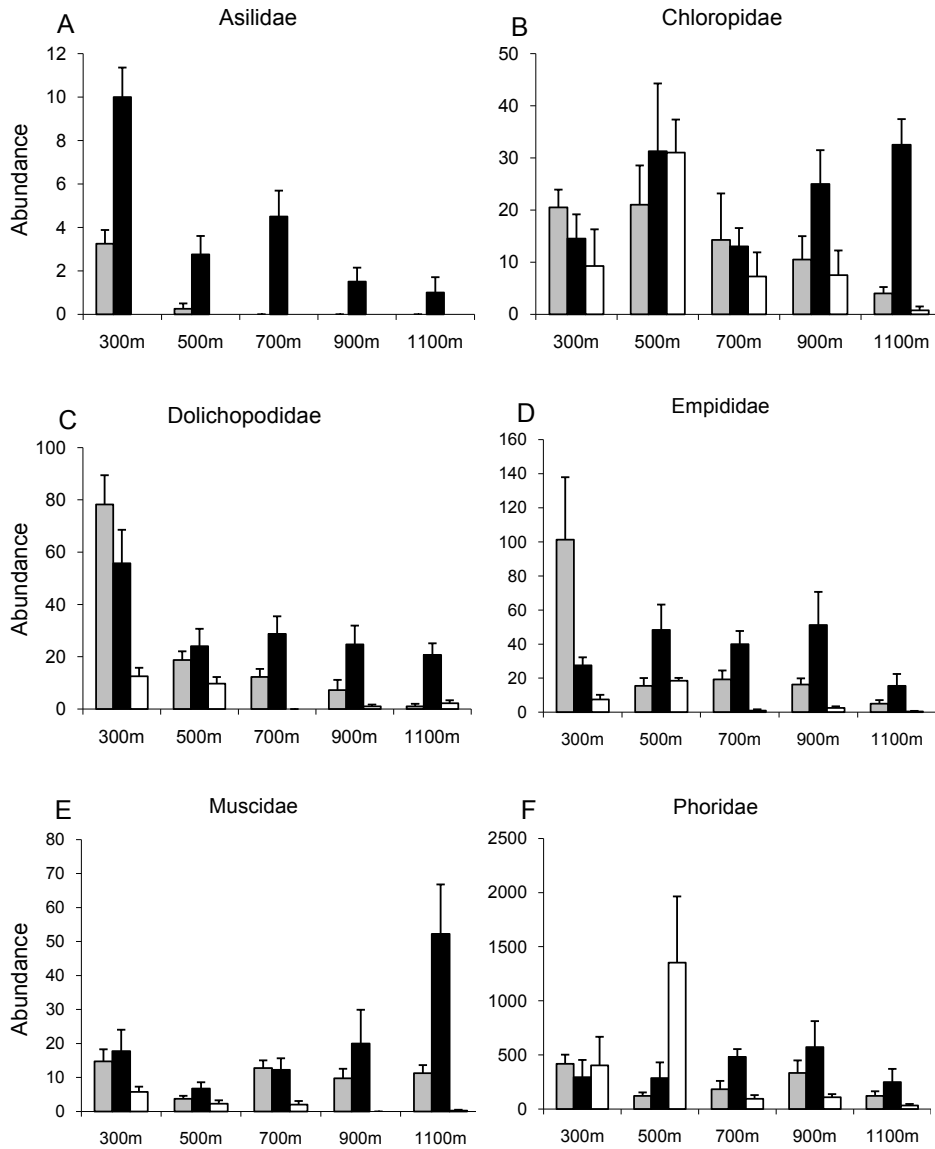


FIG. 6. Mean (+SE) abundances of the six fly families that were included in the three subsets of families selected by the Bio-Env procedure (see Results). A, Asilidae; B, Chloropidae; C, Dolichopodidae; D, Empididae; E, Muscidae; F, Phoridae.

with individual species likely to have unique responses; and 3) the limited time period (10 days) over which samples were taken (e.g. trapping could coincide with a mass emergence of a particular family in a particular location). Nonetheless, some consistent responses are apparent. First, winter (July) sees a marked decrease in abundance and family richness across all altitudes. Second, the extremes of altitude, that is the highest and lowest altitudes, tend to be most consistently different from other altitudes.

Seven brachyceran families were the most abundant; the Phoridae, Empididae, Dolichopodidae, Chloropidae, Drosophilidae, Sphaeroceridae, and Muscidae. The dominance of these families is consistent with an earlier study at Lamington National Park which also used Malaise trap samples and found the same seven families dominated the brachyceran fauna (Kitching *et al.* 2004).

The overall seasonal pattern of dipteran abundance is also consistent with those found for other surveys of tropical insects (e.g. Frith & Frith 1985; Wilson *et al.* 2007a) with flies at their most abundant in summer and lowest in winter. However, not all families followed this trend. For example, the Rhagionidae, Ephydriidae, Heleomyzidae, Lauxaniidae, Milichiidae and Sphaeroceridae were most abundant in October, possibly reflecting Spring emergences, and winter active families included the Phoridae, Chloropidae and Drosophilidae. In each of these three families, aspects of their feeding biology or habit may facilitate their success under cooler conditions. In a study of flies in subtropical rainforests, Kitching *et al.* (2005) similarly found that the schizophoran families Chloropidae, Lauxaniidae, Heliomyzidae, and Ephydriidae increased in numbers during winter. Since the majority of species in these families are not predators or fully aquatic decomposers, Kitching *et al.* (2005) suggested their resource base was maintained through the dry cooler season. In the Wet Tropics, schizophoran flies are most abundant in Spring

(October) at higher altitudes and in autumn (April) at lower altitudes (Wilson *et al.* 2007a). While we have not sorted the autumn sample (March), we observed the same trend at higher altitudes.

While the change was less consistent than that demonstrated between seasons, fly family assemblages do change across the altitudinal gradient. The majority of fly families (33 out of 46) were most abundant at the two lowest altitudes, however the Sciadoceridae, Calliphoridae, Clusiidae, Ephydriidae, Helosciomyzidae, Lauxaniidae and Muscidae were most abundant in the 1100 m samples (Table 1). Our analysis indicated that the Asilidae, Dolichopodidae, Chloropidae, Muscidae, Phoridae, and Empididae contributed most to the pattern of fly assemblages between altitudes being expressed differently across the three seasons. Each family is likely to respond to the environmental conditions in accordance with their habit or life cycle needs. There were some consistent patterns across families. For example, the predatory groups, the Dolichopodidae, Empididae and Asilidae, showed a general pattern of decreasing abundance with increasing altitude, with abundances highest in summer and lowest in winter, with Asilidae completely absent from the winter sample. Available data suggest that predation by insects decreases with increasing altitude (Hodkinson 2005). This pattern may be directly related to the decrease in prey abundance with increasing altitude. In addition, the searching efficiency of these active predators may be impaired under the cooler and often misty conditions at the higher altitudes, as has been seen in parasitoids (Coulson *et al.* 1995). Other families showed different responses to altitude across seasons. For example, the Phoridae were most common in winter, with a peak in abundance at 500 m and lowest numbers at 1100 m. While the high abundance of Phoridae in winter might indicate an ability to cope with cooler conditions, their peak abundance at 500 m and decline at 1100m shows that these decomposers of terrestrial organic matter avoid the extremes of that season by occupying warmer, moister habitats.

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The upper and lower distributional limits of a species are determined by its capacity to match its thermal tolerance range to the temperature profile of its habitat (Hodkinson *et al.* 1999). With temporal variation in temperature, the upper distributional limits of species may fluctuate on a seasonal basis (Hodkinson 2005). For example, Menendez & Gutierrez (2004) demonstrated that seasonal shifts in the distribution of species of dung beetles are linked to corresponding shifts in microclimatic conditions. The presence of any fly family at a particular altitude in a particular season is likely to reflect environmental determinants of the distribution of individual taxa within that family. For example, the presence of particular families at lower, warmer altitudes in winter and higher, cooler altitudes in summer reflects species of these families occupying the most suitable habitat throughout the year. Future research should focus on the responses of individual species and whether they also display seasonal shifts in distribution and abundance across altitude. Vegetation, humidity, rainfall, minimum and maximum temperatures, available sunlight, soil temperature, moisture and chemical composition change considerably across the IBISCA-Queensland gradient (see Strong *et al.* 2011). Any of these parameters have the potential to influence the composition and abundances of fly families through effects on the environmental requirements of immatures and adults.

CONCLUSIONS

The results of this study highlight the complex responses of the ubiquitous Diptera to changes in environmental conditions. While changing altitude, and accompanying changes in microclimate, was expected to have a pronounced effect on fly assemblages, mirroring responses expected due to future climate change, the influence of altitude was overwhelmed by seasonal variation in climate. The differential pattern observed among families gives some indication of the range of possible responses to climate change – beyond

simple decrease and increase. Further information on responses of individual species to altitude and season is likely to greatly improve our understanding of the complexity of the patterns observed here. Future studies should focus on whether there are seasonal shifts in the distribution and abundance of individual species across altitude.

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LITERATURE CITED

- Anderson M.J., Gorley R.N. & Clarke K.R. 2008. *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. (PRIMER-E: Plymouth).

- Arroyo, M.T., Primack, R. & Armesto, J.J. 1982. Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. *American Journal of Botany* **69**: 82-97.
- Botes, A., McGeoch, M.A., Robertson, H.G., van Niekerk, A., Davids, H.P. & Chown, S.L. 2006. Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography* **33**: 71-90.
- Brehm, G., Colwell, R.K. & Kluge, J. 2007. The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecology and Biogeography* **16**: 205-219.
- Brehm, G. & Fiedler, K. 2003. Faunal composition of geometrid moths changes with altitude in an Andean montane rain forest. *Journal of Biogeography* **30**: 431-440.
- Bruhl, C.A., Mohamed, V. & Linsenmair, K.E. 1999. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology* **15**: 265-277.
- Chatzaki, M., Lymberakis, P., Markakis, G. & Mylonas, M. 2005. The distribution of ground spiders (Araneae, Gnaphosidae) along the altitudinal gradient of Crete, Greece: species richness, activity and altitudinal range. *Journal of Biogeography* **32**: 813-831.
- Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**: 117-143.
- Clarke, K.R. & Gorley, R.N. 2006. *PRIMER v6: User Manual/Tutorial*. (PRIMER-E: Plymouth).
- Coulson, S.J., Hodkinson, I.D., Strathdee, A.T., Block, W., Webb, N.R., Bale, J.S. & Worland, M.R. 1995. Thermal environments of Arctic soil organisms during winter. *Arctic and Alpine Research* **27**: 365-371.
- Darling, D.C. & Packer, L. 1988. Effectiveness of malaise traps in collecting Hymenoptera: the influence of trap design, mesh size and location. *Canadian Entomologist* **120**: 787-796.
- Erwin, T.L. 1982. Tropical forests: their richness in Coleoptera and other Arthropod species. *The Coleopterists Bulletin* **36**: 74-75.
- Escobar, F., Lobo, J.M. & Halffter, G. 2005. Altitudinal variation of dung beetle (Scarabaeidae: Scarabaeinae) assemblages in the Colombian Andes. *Global Ecology and Biogeography* **14**: 327-337.
- Evans, F.C. & Owen, D.F. 1965. Measuring insect flight activity with a malaise trap. *Papers of the Michigan Academy of Science, Arts and Letters* **50**: 89-94.
- Fisher, B.L. 1996. Ant diversity patterns along an elevational gradient in the Reserve Naturelle Integrale d'Andringitra, Madagascar. *Fieldiana Zoology* **85**: 93-108.
- Fisher, B.L. 1999. Ant diversity patterns along an elevational gradient in the Reserve Naturelle Integrale d'Andohahela, Madagascar. *Fieldiana Zoology* **94**: 129-147.
- Fleishman, E., Fay, J.P. & Murphy, D.D. 2000. Upsides and downsides: contrasting topographic gradients in species richness and associated scenarios for climate change. *Journal of Biogeography* **27**: 1209-1219.
- Frith, C.B. & Frith, D.W. 1985. Seasonality of insect abundance in an Australian upland tropical rainforest. *Australian Journal of Ecology* **10**: 237-248.
- Hamilton, J., Yeates, D., Hastings, A., Colless, D., McAlpine, D., Bickel, D., Daniels, G., Schneider, M., Cranston, P. & Marshall, S. 2006. *On The Fly: The Interactive Atlas and Key to Australia Fly Families*. (Australian Biological Resources Study, Canberra & Centre for Biological Information Technology: St. Lucia).
- Hodkinson, I.D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* **80**: 489-513.
- Hodkinson, I.D., Bird, J.M., Miles, J.E., Bale, J.S. & Lennon, J.J. 1999. Climatic signals in the life histories of insects: the distribution and abundance of heather psyllids (*Strophingia* spp.) in the UK. *Functional Ecology* **13**: 83-95.
- Kearns, C.A. 1992. Anthophilous fly distribution across an elevation gradient. *American Midland Naturalist* **127**: 172-182.
- Kitching, R.L., Bickel, D. & Boulter, S. 2005. Guild analyses of Dipteran assemblages: a rationale and investigation of seasonality and stratification in selected rainforest faunas. Pp 388-415. In, Yeates, D.K. & Wiegmann, B.M. (eds), *The evolutionary biology of flies*. (Columbia University Press: New York).
- Kitching, R.L., Bickel, D., Creagh, A.C., Hurley, K. & Symonds, C. 2004. The biodiversity of Diptera in Old World rain forest surveys: a comparative faunistic analysis. *Journal of Biogeography* **31**: 1185-1200.

Variation in assemblages of flies (Diptera)

- Kitching, R.L., Putland, D., Ashton, L.A., Laidlaw, M.J., Boulter, S.L., Christensen, H. & Lambkin, C.L. 2011. Detecting biodiversity changes along climatic gradients: the IBISCA-Queensland Project. *Memoirs of the Queensland Museum-Nature* **55**(2): 235-250.
- Laidlaw, M.J., McDonald, W.J.F., Hunter, R.J. & Kitching, R.L. 2011. Subtropical rainforest turnover along an altitudinal gradient. *Memoirs of the Queensland Museum-Nature* **55**(2): 271-290.
- Lambkin, C.L., Power, N. & Starick, N.T. 2002. Mt Kosciuszko: Biodiversity of Flies (Diptera). Pp 76-87. In, Green, K. (ed.), *Biodiversity in the Snowy Mountains*. (Australian Institute of Alpine Studies: Jindabyne).
- Malaise, R. 1937. A new insect-trap. *Entomologisk Tidskrift* **58**: 149-160.
- McKie, B.G., Pearson, R.G. & Cranston, P.S. 2005. Does biogeographical history matter? Diversity and distribution of lotic midges (Diptera: Chironomidae) in the Australian Wet Tropics. *Austral Ecology* **30**: 1-13.
- Menendez, R. & Gutierrez, D. 2004. Shifts in habitat associations of dung beetles in northern Spain: Climate change implications. *Ecoscience* **11**: 329-337.
- Monteith, G.B. & Davies, V.T. 1991. Preliminary account of a survey of arthropods (insects and spiders) along an altitudinal rainforest transect in tropical Queensland. Pp 345-362. In, Werren, G. & Kershaw, P. (eds), *The Rainforest Legacy: Australian National Rainforest Study*. (Australian Government Publishing Service: Canberra).
- Novotny, V. & Basset, Y. 2000. Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos* **89**: 564-572.
- Power, N. 1998. *Temporal and spatial diversity of Therevidae in South East Queensland (Diptera: Therevidae)*. Honours Thesis. (Department of Entomology, University of Queensland: Brisbane).
- Sanders, N.J., Lessard, J.-P., Fitzpatrick, M.C. & Dunn, R.R. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography* **16**: 640-649.
- Southwood, T.R.E. 1978. *Ecological methods with particular reference to the study of insect populations*. 524 Pp. (Chapman and Hall: London).
- Strong, C.L., Boulter, S.L., Laidlaw, M.J., Maunsell, S.C., Putland, D. & Kitching, R.L. 2011. The physical environment of an altitudinal gradient in the rainforest of Lamington National Park, southeast Queensland. *Memoirs of the Queensland Museum-Nature* **55**(2): 251-270.
- Townes, H. 1962. Design for a Malaise trap. *Proceedings of the Entomological Society of Washington* **64**: 253-262.
- Townes, H. 1972. A light-weight Malaise trap. *Entomological News* **83**: 239-247.
- Warren, S.D., Harper, K.T. & Booth, G.M. 1988. Elevational distribution of insect pollinators. *American Midland Naturalist* **120**: 325-330.
- Wilson, R.D., Trueman, J.W.H., Williams, S.E. & Yeates, D.K. 2007a. Altitudinally restricted communities of schizophoran flies in Queensland's Wet Tropics: vulnerability to climate change. *Biodiversity and Conservation* **16**: 3163-3177.
- Wilson, R.J., Gutierrez, D., Gutierrez, J. & Monserrat, V.J. 2007b. An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology* **13**: 1873-1887.
- Yeates, D.K. 1985. Altitudinal transect studies at Cape Tribulation, north Queensland IV. The march flies (Diptera: Tabanidae). *Queensland Naturalist* **26**: 58-61.
- Yeates, D.K., Bickel, D., McAlpine, D.K. & Colless, D.H. 2009. Diversity, relationships and biogeography of Australian flies. Pp 227-256. In, Pape, T., Bickel, D. & Meier, R. (eds), *Diptera Diversity. Status, challenges and tools*. (Koninklijke Brill NV: The Netherlands).

