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ORIGINAL ARTICLE

The biodiversity of Diptera in Old World rain forest surveys: a comparative faunistic analysis

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ABSTRACT

Aim Identify the taxonomic patterns and the relative importance of particular families of Diptera sampled in comparative biodiversity surveys carried out at seven rain forest locations. We test and quantify the contention that different trapping methods routinely target different families. We identify the south–north (and upland/lowland) patterns and generate a set of hypotheses concerning mechanisms underlying these patterns.

Location Australia and Papua New Guinea.

Methods A total of 28,647 Diptera collected using canopy knockdown, yellow pan (water) traps and Malaise traps have been sorted to 56 families following these surveys. Comparative analyses across sites from Lamington National Park in south-east Queensland, Australia to the Kau Wildlife area in Madang Province, Papua New Guinea, of the dipteran assemblages, and separately, of the 14 families which collectively made up 95.8% of the sample, are presented.

Results Ordination by multi-dimensional scaling and analyses of variances showed that the three methods complemented each other in terms of target families and, together, sampled a large proportion of the expected fauna of these sites. Ordinations on a method-by-method basis permitted the identification of groups of sites and analyses of variance indicated which taxa differed significantly across these groups.

Main conclusions Recurrent patterns and associated hypotheses about their generation emerge from the data. These mirror floristic differences and reflect the biogeographic history of the sites since the Miocene. Clear linkages between the lowland faunas of Papua New Guinea and northern Australia are evident and are reflected in the abundances of the Dolichopodidae, Empididae, Muscidae and Tipulidae (other groupings underlined the essential difference of the New Guinean fauna which had characteristic proportions of Cecidomyiidae, Chironomidae, Dolichopodidae, Phoridae and Psychodidae). A subtropical grouping of families was evident comprising, *inter alia*, Chloropidae, Mycetophilidae, Drosophilidae and Phoridae which was frequently linked with the higher elevation tropical fauna at Robson's Creek, Atherton Tablelands. The long isolated, high elevation, rain-forested massif at Eungella, central Queensland often emerged as a unique entity in the analyses, characterized by the high numbers of and proportions of Chironomidae, Psychodidae, Tipulidae and Empididae. This study supports the case for the wider use of Diptera in biodiversity analyses, complementing extensive earlier analyses which have used, predominantly, large coleopteran assemblages. The results indicate the potential power of family-level analyses at large geographical scales and contribute to the ongoing debate on 'taxonomic sufficiency'.

Keywords
Biodiversity, Old World, Diptera, survey, rain forest.

INTRODUCTION

The enormous biodiversity of the Insecta within rain forest ecosystems is well established (Erwin, 1982; Stork, 1987; May, 1988; Wilson, 1999; Pimm, 2001). Within the class Insecta we usually designate the Coleoptera, Lepidoptera, Diptera, and Hymenoptera as 'mega-diverse' with each order conservatively estimated to contain over a million species world-wide. The sheer numbers of individuals of these (and other) orders generated by mass sampling techniques and their substantial levels of taxonomic uncertainty have made most attempts at total inventory ineffective or, at the very least, very long-term goals (Noyes, 1989; Hammond, 1990; Stork & Brendell, 1990; but see Janzen, 1992). Nevertheless for both fundamental and applied reasons these mega-diverse groups should not be ignored in any studies of forest biodiversity. A clear alternative to the 'endless' inventory approach is the use of comparative protocols in which sets of forests are sampled using a standard sampling effort applied at comparable seasons of the year (Kitching *et al.*, 2001).

Over the last 10 years we have developed such a comparative protocol (Kitching *et al.*, 2000a) which, to date, we have applied to 10 1-ha reference plots in Australasian and Asian rain forests. The protocol uses seven different arthropod-trapping techniques (two of which are applied at ground level *and* in the canopy) and has been applied at the height of the wet season in each of these locations. Kitching *et al.* (2001) present an analysis of the ordinal level results from the first four of these locations. At lower taxonomic levels, to date, results on the diversity of trees, ants and mites have been published (Walter *et al.*, 1998; Kitching *et al.*, 1999; Majer *et al.*, 2001).

The analysis of pattern in biological diversity across sites leads directly to the informed generation of hypotheses about the underlying biogeographic and ecological processes structuring particular biological assemblages (Rodgers & Kitching, 1998; Walter *et al.*, 1998) and human impacts upon them (Kitching *et al.*, 2000b). Taxonomic similarity and turnover are commonly examined in this way. Frequently such taxonomically based analyses are followed by re-analysis of the information sorted not into taxa but into meaningful trophic guilds (*sensu* Root, 1967; Simberloff & Dayan, 1991).

Among rain forest insects the Coleoptera have been the target group of choice for biodiversity analyses (Stork, 1987; Hammond *et al.*, 1996) in which taxonomic analysis is followed by investigation of guild structure. There have been several reasons for this: first, the order is ecologically diverse (in contrast, say, to the Lepidoptera, the members of which are pre-eminently phytophagous), secondly, the Coleoptera are generally sufficiently abundant in samples that even after sorting to family or subfamily level numbers remain sufficiently high to preserve statistical analytical power and, finally, there is a good correspondence between family or subfamily designation and membership of particular feeding guilds.

All of these advantages, however, also pertain to the Diptera with the added advantage that there are rather fewer families yet more guilds involved. The sorting task is accordingly more straightforward and, arguably, the ecological functionality that is 'captured' is greater. We hasten to add that identification keys for Diptera are no simpler than those for any other order but a very large proportion of any sample can be sorted to family given a familiarity with as few as 15 such taxa. In addition, for most sampling methods, the numbers of Diptera caught are customarily considerably greater than for other orders (including the Coleoptera) with concomitant increase in the robustness of statistical analyses which involve them. Yet the Diptera have been virtually ignored in studies of terrestrial biodiversity (Didham, 1998; Hurtado Guerrero *et al.*, 2003; but see, Disney, 1986; Disney *et al.*, 1982).

This paper presents an analysis of extensive samples of Diptera collected using three sampling methods – canopy knockdown, Malaise traps and yellow pan (water) traps – from seven of the eight locations we have sampled in Australasia. Taxonomic patterns are analysed and the relative importance of particular families are identified in consequence. We test and quantify the contention that different trapping methods routinely target different families. We identify the south–north (and upland/lowland) patterns and generate a set of hypotheses concerning the mechanisms underlying these patterns.

The results presented also bear on the 'taxonomic sufficiency' debate (Pik *et al.*, 1999; Guerold, 2000; Lenat & Resh, 2001; King & Richardson, 2002). In particular, we show that useful, interpretable and interesting patterns emerge in the relative abundances of dipteran families when analysed, as here, *at a continental scale*. We acknowledge that much further information is likely to emerge when (or if) analyses of our samples becomes possible at infra-family levels. As with many rain forest taxa the crucial word here is 'if' given the current inadequacies and likely continued decline in the availability of taxonomic expertise for most key families. For *finer scale analyses* – across adjacent catchments, within archipelagos, across co-occurring land-uses, and so forth – the answering of key questions concerning the phenomenology, generation and maintenance of biodiversity will require finer levels of taxonomic resolution (e.g. Kitching *et al.*, 2000b).

METHODS, STUDY SITES AND ANALYSES

The results are presented for Diptera collected from seven sites we have surveyed to date. The locations of these sites are indicated in Fig. 1. At all sites a hectare of more or less undisturbed rain forest was selected and a complete vegetation

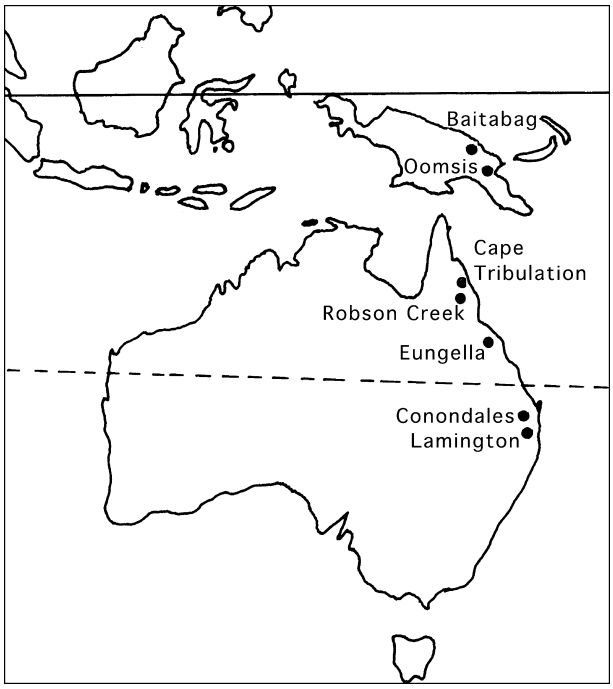

Figure 1 Map showing the location of each of the Australasian rain forest study sites.

survey (for stems >5 cm d.b.h.) carried out. Arthropods were sampled at each site using seven different methods. Each trapping method was spatially replicated at least three times within the hectare with trap locations located randomly within each plot. A comparative analysis of the orders trapped by each method is presented in Kitching *et al.* (2000a, 2001). On the basis of these results we have used the samples obtained from pyrethrum canopy-knockdown, from Malaise traps at ground level, and from water-filled yellow-pan traps at ground level for the analyses of Diptera presented here. A detailed account of the full sampling protocol is available in Kitching *et al.* (2000a).

Sampling methods

Canopy knockdown sampling

Three canopy pyrethrum knockdown samples were collected within each of the targeted hectares once all other arthropod sampling had been completed. In each case a line was shot as high as possible into a canopy tree. A 10 × 10 m site was established based around the line and between 15 and 20 0.5 m^2 collecting funnels were deployed within this site and under many different species of trees. A Stihl SG-17^{TM} (Stihl Pty Ltd., Knoxfield, Melbourne, Victoria, Australia) spraying machine was hauled into the canopy and run for 5 min, filling the adjacent canopy with natural pyrethrum fog (using a Rudchem PyFog^{TM} formulation, (Rudduck Pty Ltd., Port Melbourne, Victoria, Australia) the active constituents of which are 4 gm L^{-1} pyrethrins, 12 g L^{-1} piperonyl butoxide and 979 g L^{-1} hydrocarbon liquid, diluted 1 : 30 with water according to the manufacturers' recommendations). The arthropods knocked down by the insecticide were collected for 4 h. Each of the three spraying locations was selected so that the sampling activity at one was unlikely to interfere with that at either of the others.

Malaise trap sampling

Three Townes' design Malaise traps (Townes, 1962) were erected at ground level and exposed for a total of at least 4 days at each site. Our traps were of a standard design constructed of light-weight black and white nylon mesh. Each collecting vessel contained a short length of insecticide-impregnated soft plastic as a killing agent. The traps were emptied daily over a 4-day period and the catches transferred to ethanol for sorting. We are aware that the use of particular killing agents in Malaise traps (whether dichlorvos, as in this case, or ethanol) may affect the composition of the insect taxa caught. However, in a comparative analysis, in which the results of a set of trapping methods applied in an identical fashion across sites are compared, this bias is irrelevant.

Yellow pan (water) trap sampling

Yellow-painted, plastic containers, each 16.5 × 19.5 × 5 cm deep, were placed on the ground within each plot (six at the Lamington site, 10 at each of the other sites). Each was half-filled with water to which two drops of household detergent had been added to reduce the surface tension of the water and hence cause floating insects to sink. These were visited daily for a minimum of 4 days and their daily catches filtered into ethanol.

All specimens have been deposited at the Australian Museum Sydney where they are available for further collaborative analysis by appropriate specialists (contact D. Bickel).

Study sites

Information for the Lamington, Conondales, Eungella and Robson Creek is collated from Laidlaw (1999). Data for the Cape Tribulation site is compiled from Kitching *et al.* (1993), McIntyre *et al.* (1994) and unpubl. data (M. Laidlaw, R.L. Kitching). Details for the New Guinea sites are extracted from Laidlaw *et al.* (2004).

Lamington National Park, south-east Queensland ('Lamington')

The study site is located close to Green Mountains, Lamington National Park, in south-east Queensland (28°13′ S 153°07′ E) at 600 m a.m.s.l. The substrate is a combination of laterite and basalt. The local climatic regime contrasts cool, drier winters with warm wet summers (annual mean rainfall 1623 mm, annual maximum 31.2 °C, minimum 2.8 °C, mean monthly range 11.2–25.7 °C). The forest type is complex notophyll vine forest (*sensu* Webb *et al.*, 1984) and the tree flora of the site has been described in detail by Laidlaw *et al.*

(2000) and by McDonald & Whiteman (1979). The tree flora (> 5 cm d.b.h.) of the plot comprised 1266 stems of 76 species. The most abundant tree species were *Actephila lindleyi* (Steud.) Airy Shaw, *Randia benthamiana* F. Muell. and *Baloghia inophylla* (G. Forst.) P.S. Green although, in terms of basal area, the site was dominated by *Argyrodendron actinophyllum* (F.M. Bailey) Edlin, *A. trifoliolatum* F. Muell., *Pseudoweinmannia lachnocarpa* (F. Muell.) Engl., *Caldcluvia paniculosa* (F. Muell.) Hoogland and *Ficus watkinsiana* F.M. Bailey. Floyd (1990) designated the vegetation as an *Argyrodendron trifololatum–A. actinophyllum–Caldcluvia paniculosa* tall closed-forest alliance.

Conondales National Park, south-east Queensland ('Conondales')

The 1-ha plot was established in Belthorpe State Forest, south-east Queensland (26°44′ S 152°36′ E) at 720 m a.m.s.l. The local soil type is complex derived from a combination of basic and acidic igneous substrates, metamorphic rocks and alluvia in ravines. The local climate is similar to that at Lamington with cool, drier winters and warm wet summers (annual mean rainfall 1345 mm, annual maximum 34.2 °C, minimum 3.7 °C, mean monthly range 13.6–26.6 °C). The vegetation is classified as complex notophyll vine forest (Roberts, 1977). The plot has 1313 stems > 5 cm d.b.h. belonging to 51 species. The site was dominated by *Niemeyera chartaceae* (F.M. Bailey) C.T. White. Other species with high importance scores were *Archontophoenix cunninghamiana* (H. Wendl.) H. Wendl. & Drude, *Cyathea leichardtiana* (F. Muell.) Copel., *Argyrodendron trifoliolatum* and *Sloanea australis* (Benth.) F. Muell.

Eungella National Park, central Queensland ('Eungella')

The study site is located at Mt Dalrymple in Eungella National Park, Queensland (21°01′ S 148°37′ E) at an altitude of 720 m a.m.s.l. The Eungella massif represents an ancient isolated block of central Queensland rain forest, now much reduced by logging. It receives, on average 1699 mm of rain annually, a mean monthly temperature range of 16.7–27.8C with an annual maximum of 34.8 °C and minimum of 6.4 °C. The complex notophyll vine forest of the plot is characteristic of ridges and less fertile soils within the region. The surveyed hectare had 1983 stems > 5 cm d.b.h. belonging to 51 species. The numerically dominant species were, in descending order of importance, *Cryptocarya densiflora* Blume, *Archontophoenix alexandrae* (F.Muell.) H.Wendl. & Drude, *Syzygium erythrodoxum* (S.Moore) B.Hyland, *Syzygium wilsoni* (F.Muell.) B. Hyland and a further unidentified species of *Cryptocarya.*

Robson Creek, Danbulla State Forest, north Queensland ('Robson Creek')

The Robson Creek plot is located in Danbulla State Forest on the Atherton Tablelands of north Queensland (17°06′ S 143°37′ E) at an altitude of 686 m a.m.s.l. The site has a substrate of granitic origin but an important granite/basalt intersection occurs just south of the plot. The climate in the area contrasts warm, wet summers with mild, drier winters. The region receives on average 1394 mm of rainfall annually. Mean monthly temperatures range from 15 to 25.5 °C. The mean annual maximum temperature is 29.9 °C and the minimum, 7.6 °C. The vegetation on the plot is again complex notophyll vine forest. The hectare contained 1207 stems >5 cm d.b.h. representing 113 species. The most dominant species numerically, in descending order, were *Daphnandra repandula* (F.Muell.) F.Muell., *Sloanea australis* (Benth.) F. Muell, *Litsea leeeiana* (F.Muell.) Merr., *Syzygium trachyphloium* (C.T. White) B. Hyland and *Bielschmiedia tooram* (F.M. Bailey) B.Hyland.

Cape Tribulation, north Queensland ('Cape Tribulation')

The study plot at Cape Tribulation was located adjacent to the site of the north Queensland Canopy Crane facility close to the village of Cape Tribulation, north Queensland (16°06′ S, 145°27′ E, 81 m a.m.s.l.). It receives an annual rainfall of about 2500 mm and experiences an average daily temperature range from 22 to 28 °C. The complex notophyll vine forest on the plot received the full force of Cyclone 'Rona' 3 years before our survey. The hectare supported 1538 trees greater than 5 cm d.b.h. belonging to 137 species. The dominant species, numerically, were *Macaranga subdentta* Benth., *Cleistanthus myrianthus* (Hassk.) Kurz, *Brombya platynema* F.Muell. and *Licuala ramsayi* (F.Muell.) Domin. The soils of the area are a range of alluvials.

Oomsis experimental forest, Morobe Province, Papua New Guinea ('Oomsis')

The Oomsis plot is located close to its eponymic village west-north-west of Lae in Morobe Province, Papua New Guinea (6°41′ S 146°48′ E) at 65 m a.m.s.l. It receives an annual rainfall of 1979 mm and experiences a temperature range from 21.6 to 32.3 °C. Paijmans (1975) describes the forest as 'medium crowned lowland hill forest'. The 1-ha plot contained 1020 stems of 121 species. The dominant species were *Medusanthera laxiflora* (Miers) Howard, *Lepidopetalum* sp., *Pandanus* sp., *Celtis latifolia* Planch. and *C. philippinensis* Bico.

Kau Wildlife area, Baitabag, Madang Province, Papua New Guinea ('Baitabag')

The study plot was located within the Kau Wildlife area of Madang Province adjacent to the village of Baitabag in Papua New Guinea (5°08′ S 145°47′ E) at 100 m a.m.s.l. On a principally alluvial substrate the area receives a mean annual rainfall of 1972 mm and experiences a temperature range from 23.1 to 30 °C (McAlpine *et al.*, 1975). The vegetation of the area is a mosaic of secondary growths of various ages reflecting the shifting cultivation practices of the region (Paijmans, 1975). The surveyed hectare contained 1042 stems > 5 cm d.b.h. belonging to 152 species. In descending order the

numerically dominant species were *Pimelodendron amboinicum* Hassk., *Pometia pinnata* J. R. Forster & J. G. Forster, *Dysoxylon pettigreweanum* Bailey, *Erythrospermum candidum* (Beccari) Beccari and *Horsfieldia irya* Warb.

Analyses

The basic description of the fauna encountered in our samples addresses the entire data set as do the ordinations. The analyses of variance were carried out on a reduced data set comprising the 14 families which together made up 95.8% of the individuals encountered.

Two basic questions were tackled using the data generated in this study. Basic differences in the target groups of each of the three sampling methods were examined by comparison of the family profiles obtained using each sampling method across all sites combined. Secondly, and of much greater interest, the differences in the profiles from site to site for each of the three sampling methods have been examined.

In order to answer these questions multivariate analyses of the data pooled across methods, and for each method in turn have been carried out. Ordination using semi-strong hybrid multi-dimensional scaling (MDS) (Belbin, 1995) was used to search each of the data sets for pattern. Two-dimensional ordinations were obtained to indicate overall differences between sampling methods and across sites for each of the three sampling methods. Following ordinations, analyses of similarity (ANOSIM) were carried out based on the centroids of each category of observations (methods, or sites within methods, respectively). This analysis allowed the calculation of an ANOSIM *F*-value and an associated probability.

Following the ordination, two-way analyses of variance examining the importance of site, sampling method and their interaction, have been carried out on the data for the 14 targeted families. Analyses have been carried out on standard measures of Shannon Diversity (H'), evenness (E) and richness (S) of counts across families (see Magurran, 1988 for the standard formulae used), as well as on both simple counts of individuals within each family and on the proportions represented by each family in each sample (arcsine square root transformed). Significant results were further investigated using Least Significant Difference tests. Because multiple tests were carried out on elements of the same data set, a critical *P* value of 0.001 was adopted to avoid type 1 errors. This represents a more stringent requirement than indicated by most formal Bonferroni corrections.

The necessity to examine the data using both raw abundances and relative proportions of each taxa reflect a basic dilemma in all assemblage-based work of this sort. Raw abundances are, statistically, to be preferred: they are the 'actual' data, and each count is, *a priori*, unweighted both in itself and in terms of the other counts. However when sampling is, inevitably, carried out at different times in different places raw counts may produce patterns which reflect the local sampling milieu at the particular site and time, rather than any fundamental differences among assemblages. However as, in community ecology, we try to distinguish features which differentiate one *set* of taxa from another (i.e. we are taking a fundamentally multivariate approach) then it is the *relative* representation of a particular taxon that may tell us something about the importance of that entity in the full assemblage at the time of sampling. Of course the calculation of proportions means that individual counts of particular taxa inevitably affect the values calculated for all other taxa and the values arrived at may owe more to, say, a single large count than is entirely desirable. Further, proportions of particular taxa may also reflect immediate sampling conditions rather than 'real' differences between communities. We suggest that these two disadvantages are minimized when an appropriate taxonomic level is chosen, when overall counts are high and when the number of categories (i.e. taxa) is also relatively large. Insights are to be gained by examining the results of analyses of both counts and proportions: we choose to place more stress on the proportion-based results. We are aware, of course, that differences between the catches obtained from particular plots may reflect the vagaries of sampling at different times (although not in different seasons) and inevitable physical contrasts between plots rather than any more interesting deterministic relationships. We address this issue in the Discussion: suffice it to say here, that the huge effort involved in surveys of this kind and the fact that rain forests are patchily distributed presents logistical problems that challenge attempts to conform to precise statistical norms.

All multivariate analyses were carried out using the PATN analytical package (Belbin, 1995). Analyses of variance employed the SAS^{TM} package (SAS Institute Inc., 1990).

RESULTS

The basic data

Table 1 contains a family-by-family summary of the total individuals sampled by each method at each site. The families are ordered taxonomically following Colless & McAlpine (1991). A total of 56 families was encountered in the 28,647 specimens analysed. Of these 56 families, 22 were represented by less than 10 individuals and six by but a single individual. Canopy knockdown methods produced a sample of 2679 individuals of 41 families. The Malaise traps caught 20,469 individuals of 49 families. Yellow pan trapping generated 5499 individuals of 35 families. Individual sites generated between 2072 (Oomsis) and 8653 (Cape Tribulation) individuals (mean 4092.4 ± 869.32). The most abundant families overall were, in descending order, the Phoridae, Cecidomyiidae, Chironomidae and Sciaridae, each of which was represented by more than 2000 individuals. It is apparent immediately that the Malaise traps caught between four and eight times more individuals than the other trapping methods. When the Malaise trap data were rarefied by randomized resampling to a sample size of 3000 individuals (i.e. to be more comparable with the canopy knockdown and yellow pan trapping) then 36 families were encountered. Using this rarefied data the diversity of the three catches can be compared more legitimately: the canopy knockdown traps gave the most

Table 1 The numbers of Diptera obtained by canopy knockdown sampling, Malaise and yellow pan (water) traps from seven Australasian rain forest sites. See text for sampling details

	Lamington, Qld			Conondales, Qld			Eungella, Qld			Robson Creek, Qld			Cape Tribulation, Qld			Oomsis, PNG			Baitabag, PNG			
Taxon	Knockdown	Malaise	Yellow pan	Knockdown	Malaise	Yellow pan	Knockdown	Malaise	Yellow pan	Knockdown	Malaise	Yellow pan	Knockdown	Malaise	Yellow pan	Knockdown	Malaise	Yellow pan	Knockdown	Malaise	Yellow pan	Family totals
Nematocera	461	1779	120	63	1669	61	248	1680	730	104	714	57	460	2938	282	254	555	86	140	2221	410	15,032
Tipulidae	4	11	2	9	173	1	27	367	45	8	50	4	5	43	0	4	14	1	2	35	4	809
Trichoceridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
Dixidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Culicidae	0	0	1	1	0	0	4	0	4	0	5	0	0	8	0	6	I5	0	2	14	19	79
Chironomidae	147	120	33	4	183	19	76	286	218	24	40	4	312	1605	221	19	40	26	18	179	86	3660
Ceratopogonidae	32	4	0	11	50	1	29	26	14	7	21	2	95	155	14	33	59	5	44	442	58	1102
Simulidae	0	0	0	0	0	0	0	0	0	0	0	4	1	0	0	0	0	0	0	3	0	8
Psychodidae	12	93	1	3	0	10	14	168	368	7	96	16	3	203	26	2	79	27	7	407	69	1611
Anisopodidae	0	0	0	0	0	0	1	12	0	0	5	0	0	3	1	0	0	0	0	0	3	25
Scatopsidae	0	0	0	0	0	0	0	1	0	0	0	0	4	0	0	2	4	0	1	0	2	14
Bibionidae	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	3
Cecidomyidae	202	889	23	14	639	16	55	359	46	41	221	19	16	764	13	37	222	13	31	647	82	4349
Sciaridae	62	243	60	20	244	12	32	338	31	17	152	7	24	131	2	149	111	13	31	391	54	2124
Mycetophilidae	2	419	0	1	380	2	9	122	4	0	124	1	0	24	5	2	11	1	2	103	33	1245
Brachycera	31	566	134	44	548	208	251	1466	252	10	1042	622	107	3990	876	290	265	622	216	1036	1039	13,615
Orthorrhapha	13	33	24	13	121	32	52	114	60	6	196	19	13	254	27	38	81	131	5O	114	102	1493
Rhagionidae	0	0	0	0	1	0	0	1	1	0	0	0	0	4	0	0	2	0	0	0	0	9
Tabanidae	0	1	0	0	1	0	0	3	0	0	12	0	1	7	0	0	0	0	0	11	0	36
Stratiomyidae	1	2	0	3	11	0	0	1	0	0	3	6	2	0	0	2	2	0	2	4	0	39
Xylomyiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Therevidae	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Asilidae	0	0	2	0	9	0	3	3	1	1	4	2	0	0	0	1	1	I	0	3	0	31
Bombylidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Empididae	8	20	13	1	54	13	23	42	27	1	32	2	1	34	1	6	6	63	0	30	4	381
Dolichopodidae	4	9	9	9	43	19	26	64	31	4	145	9	9	209	26	29	69	67	48	65	98	992
Cyclorrhapha–Aschiza	8	473	44	12	191	49	44	875	89	2	497	66	21	3128	764	75	146	152	59	738	387	7820
Platypezidae	0	0	8	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	12
Phoridae	8	473	36	11	189	49	43	870	88	2	497	66	19	3124	764	75	145	152	59	734	387	7791
Pipunculidae	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Syrphidae	0	0	0	0	1	0	0	2	1	0	0	0	2	4	0	0	1	0	0	2	0	13
Cyclorrhapha–Schizophora	10	60	66	19	236	127	155	477	103	2	349	537	73	608	85	177	38	339	107	184	550	4302
Conopidae	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	6
Sepsidae	0	0	0	0	0	0	2	5	26	0	0	23	5	44	0	0	0	0	0	0	5	110
Lauxanidae	4	3	0	1	1	3	3	9	1	0	5	3	2	3	3	3	1	22	7	5	17	96
Lonchaeidae	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	5
Platystomatidae	0	0	0	0	12	0	0	2	0	0	17	0	0	6	0	0	0	9	0	7	11	64
Pyrgotidae	0	0	0	0	152	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	152
Tephritidae	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	1	5
Pseudopomyzidae	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
Cypselosomatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	2
Neriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	2	0	0	1	0	6

Micropezidae	0	0	0	0	1	0	1	0	0	0	7	96	1	10	8	0	1	1	0	1	0	127
Heleomyzidae	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Sphaeroceridae	0	9	38	1	24	85	13	19	32	0	65	81	5	262	16	5	4	11	20	29	106	825
Clusiidae	0	2	0	0	0	0	0	3	0	0	8	0	6	0	0	0	0	0	0	0	1	20
Agromyzidae	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Fergusoniidae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Periscelidae	0	0	0	1	0	0	1	4	2	0	0	0	1	0	0	0	0	1	1	1	0	12
Teratomyzidae	0	10	1	0	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	15
Ephydridae	0	0	0	0	0	0	0	0	0	0	0	0	1	6	4	2	1	1	0	6	2	23
Drosophilidae	0	5	5	3	8	1	76	347	26	1	35	267	2	153	30	17	16	36	51	96	289	1464
Cryptochetidae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Milichiidae	0	1	0	0	3	0	0	5	0	0	10	0	4	2	2	43	2	1	12	6	1	92
Chloropidae	6	16	16	12	12	3	45	30	6	1	10	23	43	35	12	104	8	250	15	21	111	779
Asteiidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Anthomyiidae	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Muscidae	0	9	3	0	7	34	2	30	2	0	84	43	0	72	10	0	3	2	0	8	5	314
Calliphoridae	0	1	3	0	6	0	1	11	5	0	100	1	0	5	0	0	0	1	0	0	0	134
Sarcophagidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2
Tachinidae	0	0	0	0	6	1	1	6	3	0	1	0	0	7	0	1	0	3	0	1	0	30
Sample totals	492	2345	254	107	2217	269	499	3146	982	114	1756	679	567	6928	1158	544	820	708	356	3257	1449	28,647

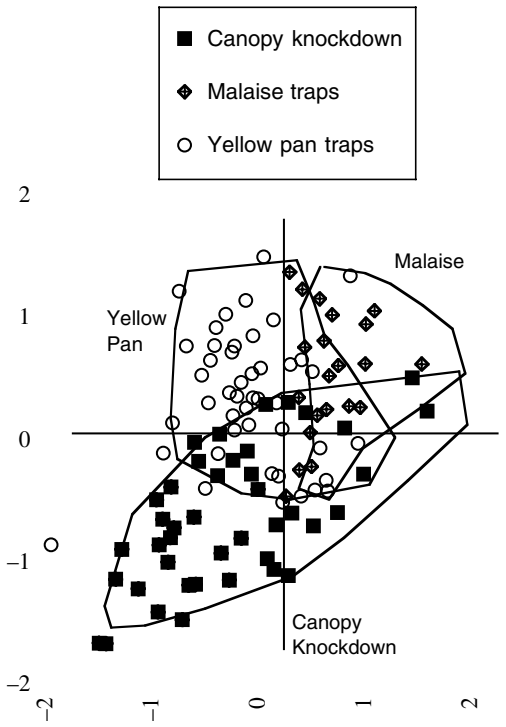

Figure 2 Ordinations using multi-dimensional scaling for the three sampling methods at each of the seven sampling sites. Squares, canopy knockdown; diamonds, Malaise traps; circles, yellow pan traps.

diverse catches with 65.3 individuals per family, the Malaise traps had 85.7 individuals per family, and the yellow pan traps 157.1 individuals per family.

Methods across sites

Figure 2 is the result of the analysis by MDS of the data collected across all seven sites by each of the three methods. The points for each of the three sampling methods show considerable cohesion with overlap in the central area of the graph space. The further analyses of these data by ANOSIM produce a highly significant result ($P < 0.0001$) confirming the likely 'reality' of the groupings shown in the figure. Because the outcomes of many individual traps were used in this analysis there are outliers from the clusters of results for each trapping type. This is particularly the case for the yellow pan traps (of which, in any case, there were considerably more replicates each time). This variability accounts for the relatively high stress value obtained in this analysis (0.27).

The results of the two-way analyses of variance carried out are summarized in Table 2. The overall measure of richness (S) differed significantly across all methods with Malaise exceeding canopy knockdown exceeding yellow pan traps. Evenness (E) was significantly lower in catches from Malaise traps than for those obtained by either of the other methods. Shannon diversity measures (which combine richness and evenness) did not differ significantly across methods.

Table 2 Summary of results of the analyses of variance carried out on the abundances and proportions of the 14 most dominant families in the Diptera data set

Response variable	Site (*P*)	Method (*P*)	Site × method (*P*)	Method differences	Site differences
H	7.82 (< 0.0001)	2.50 (= 0.0878)	3.02 (= 0.0014)	3,1,2	5 < 6,1,7,4,2 < 3
E	11.16 (< 0.0001)	10.44 (< 0.0001)	1.50 (= 0.1406)	2 < 1,3	5 < 7,6 < 1,3,4,2
S	12.90 (< 0.0001)	179.87 (< 0.0001)	5.34 (< 0.0001)	3 < 1 < 2	1,4,2 < 6,5 < 7,3
Abundance results					
Cecidomyidae	10.83 (< 0.0001)	363.55 (< 0.0001)	6.12 (< 0.0001)	3 < 1 < 2	6,4 < 3,2,5,7 < 1
Ceratopogonidae	25.19 (< 0.0001)	161.37 (< 0.0001)	17.08 (< 0.0001)	3 < 1 < 2	4,1 < 2,3,6 < 5 < 7
Chironomidae	42.50 (< 0.0001)	131.40 (< 0.0001)	17.44 (< 0.0001)	3 < 1 < 2	4,6,2 < 7,1 < 3 < 5
Chloropidae	20.40 (< 0.0001)	6.72 (< 0.0001)	6.70 (< 0.0001)	3 < 2,1	4,2,1 < 3,7,5 < 6
Dolichopodidae	9.79 (< 0.0001)	88.31 (< 0.0001)	7.41 (< 0.0001)	3,1 < 2	1 < 2 < 3,4 < 6,5,7
Drosophilidae	22.29 (< 0.0001)	25.14 (< 0.0001)	11.25 (< 0.0001)	1,3 < 2	1,2 < 6 < 4,5 < 7,3
Empididae	6.48 (< 0.0001)	64.36 (< 0.0001)	5.56 (< 0.0001)	1,3 < 2	7,5,4,6,1 < 2,3
Muscidae	12.40 (< 0.0001)	67.92 (< 0.0001)	7.75 (< 0.0001)	1 < 3 < 2	6,7,1 < 2,3 < 5,4
Mycetophilidae	11.69 (< 0.0001)	304.13 (< 0.0001)	19.08 (< 0.0001)	3,1 < 2	6,5 < 4,7,3 < 2,1
Phoridae	12.04 (< 0.0001)	121.66 (< 0.0001)	8.71 (< 0.0001)	1,3 < 2	2,6,4,1 < 3,7 < 5
Psychodidae	18.18 (< 0.0001)	92.75 (< 0.0001)	8.32 (< 0.0001)	1,3 < 2	2 < 6,1,4,5 < 3 < 7
Sciaridae	10.35 (< 0.0001)	290.90 (< 0.0001)	6.02 (< 0.0001)	3 < 1 < 2	5,4 < 2,6 < 3,1,7
Sphaeroceridae	9.73 (< 0.0001)	40.00 (< 0.0001)	17.02 (< 0.0001)	1 < 3 < 2	6,1 < 2,3,4,7 < 5
Tipulidae	32.24 (< 0.0001)	248.43 (< 0.0001)	18.75 (< 0.0001)	3 < 1 < 2	1,6,7,5 < 4 < 2 < 4
Proportion results					
Cecidomyidae	16.18 (< 0.0001)	81.55 (< 0.0001)	4.67 (< 0.0001)	3 < 1,2	5 < 3,6,7,2 < 4 < 1
Ceratopogonidae	11.21 (< 0.0001)	64.58 (< 0.0001)	2.84 (= 0.0025)	3 < 2 < 1	1,4 < 3,2,6 < 5 < 7
Chironomidae	23.99 (< 0.0001)	7.74 (= 0.0008)	3.79 (= 0.0001)	2,3 < 1	6,4,7,2 < 1,3 < 5
Chloropidae	22.32 (< 0.0001)	13.60 (< 0.0001)	5.12 (< 0.0001)	2 < 3,1	1,4,3,2,5,7 < 6
Dolichopodidae	6.80 (< 0.0001)	0.18 (= 0.8354)	1.75 (= 0.0698)	2,1,3	1 < 4,5,3,2 < 7,6
Drosophilidae	32.79 (< 0.0001)	9.58 (= 0.0002)	11.14 (< 0.0001)	2,1 < 3	2,1 < 5 < 6 < 3,4 < 7
Empididae	8.89 (< 0.0001)	1.24 (= 0.2950)	2.49 (= 0.0076)	1,2,3	5,7,4 < 1,6,2 < 3
Muscidae	13.89 (< 0.0001)	12.29 (< 0.0001)	3.48 (= 0.0003)	1 < 2,3	6,7,1,3,5 < 2 < 4
Mycetophilidae	5.10 (= 0.0002)	78.65 (< 0.0001)	8.23 (< 0.0001)	1,3 < 2	5,6 < 4,3,7 < 1,2
Phoridae	7.94 (< 0.0001)	15.70 (< 0.0001)	3.02 (= 0.0014)	1 < 3,2	2,1,4 < 3,6,7 < 5
Psychodidae	11.95 (< 0.0001)	4.07 (= 0.0205)	4.58 (< 0.0001)	1 < 3,2	2,5,1 < 6,4,7 < 3
Sciaridae	17.77 (< 0.0001)	33.73 (< 0.0001)	5.91 (< 0.0001)	3 < 2,1	5 < 4,3,7 < 2,6 < 1
Sphaeroceridae	13.95 (< 0.0001)	35.16 (< 0.0001)	6.11 (< 0.0001)	1,2 < 3	6 < 5,1,3 < 4,7,2
Tipulidae	22.51 (< 0.0001)	35.34 (< 0.0001)	3.77 (< 0.0001)	3 < 1,2	5,7,1,6 < 4 < 2 < 3

Each element in the table shows the *F* value obtained and its associated probability value. Index key: H – Shannon diversity index, E – evenness, S – family richness. Method codes: 1 – canopy knockdown, 2 – Malaise traps, 3 – yellow pan traps. Site codes: 1 – Lamimgton, 2 – Conondales, 3 – Eungella, 4 – Robson Creek, 5 – Cape Tribulation, 6 – Oomsis, 7 – Baitabag. See text for further discussion.

The analyses of *abundances* shows significant effects of 'method' for all 14 families that have been targeted. Kruskal–Wallis analyses showed that all methods differed significantly from each other for seven of the families examined. In all seven, Malaise traps caught significantly more than the other two methods. In five cases catches by canopy knockdown exceeded those in yellow pan traps but in two cases the reverse pattern was observed. Six other families (see Table 2) showed comparable numbers in the catches from canopy knockdown and yellow pan traps. These results reflect the substantially larger catches overall obtained by the Malaise traps (see above).

In general, significant differences in the *proportions* of families tended to group methods in a pairwise fashion. Only for the Ceratopogonidae did the proportional representation differ significantly across all three methods (canopy knockdown > Malaise > yellow pan traps). Knockdown sampling and Malaise traps produced statistically similar proportions of Cecidomyidae, Sciaridae and Tipulidae (all higher than in yellow pan traps) and of Drosophilidae and Sphaeroceridae (lower than in yellow pan traps). Knockdown sampling and yellow pan traps produced similar proportions of Chloropidae (higher than Malaise traps) and Mycetophilidae (lower than Malaise traps). Finally, Malaise traps and yellow pan traps caught similar proportions of Muscidae, Phoridae and Psychodidae (all higher than canopy knockdown catches) and of Chironomidae (lower than in canopy knockdowns). Interestingly the two predatory groups, Dolichopodidae and Empididae, did not differ in their proportional representation across the three methods.

Site effects within methods

Figures 3–5 illustrate the results of the ordinations for the canopy knockdown samples, the Malaise traps catches and the yellow pan traps respectively. The associated ANOVAR results

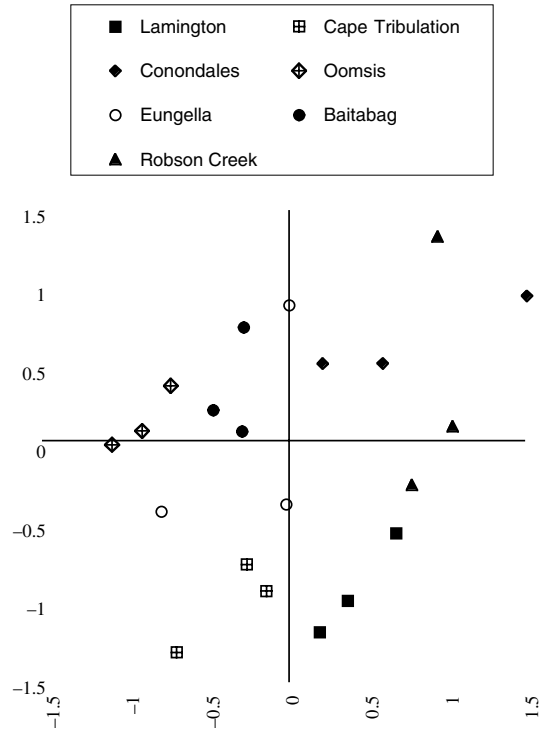

Figure 3 The ordination by multi-dimensional scaling of the results of the canopy knockdown sampling across study sites.

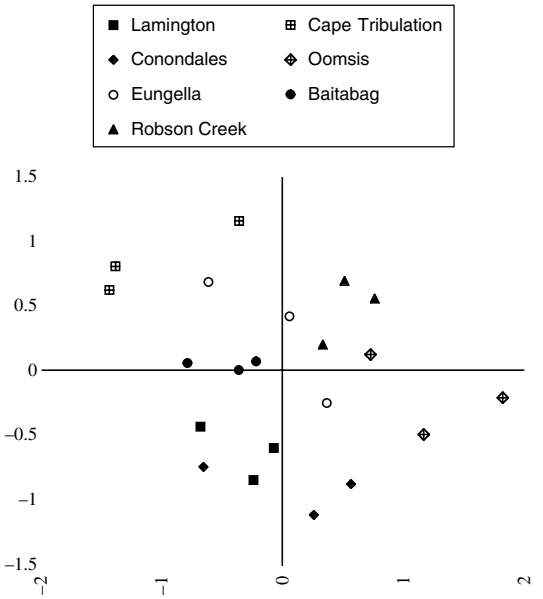

Figure 4 The ordination by multi-dimensional scaling of the results of Malaise trapping across study sites.

are summarized in Table 2. In examining the results of these analyses we have borne in mind three inter-related hypotheses derived from current biogeographical ideas which relate to history of the Australian fauna. We return to these and their potential underlying mechanisms in the 'Discussion' but state them here to inform the presentation of our results:

1 To what degree are the tropical lowland sites of northern Australia and New Guinea related to each other? And, conversely, for what taxa is their significant dissimilarity across the Torres Strait and New Guinean cordillera?

2 What is the reality and role of the subtropical element within dipteran assemblages? To what degree can the upland rain forest assemblages north of the Tropic of Capricorn be regarded as subtropical in facies, nature and history?

3 How important is the geographical and temporal isolation of the Eungella massif in generating significantly different assemblages?

Canopy knockdown samples

Figure 3 shows the results of the ordination analysis of the data from the canopy knockdown sampling. The plot shows strong pattern with a stress value of 0.199. The ANOSIM analysis is highly significant ($P < 0.0001$). The plot divides the sites into a right-hand and a left-hand half. The right-hand sector links together the two sets of subtropical sites (Lamington and the Conondales) with the higher elevation tropical site (Robson Creek). The lowland tropical sites (the two New Guinea sites plus Cape Tribulation) are clearly grouped on the left-hand half of the plot. As in most of these ordinations the Eungella results (mid-tropical, high elevation) are somewhat inconsistent and fall between the New Guinean and lowland Australian tropical sites on the right-hand side of the plot.

These results give credence to the idea that the lowland tropical sites (Baitabag, Oomsis and Cape Tribulation) show a

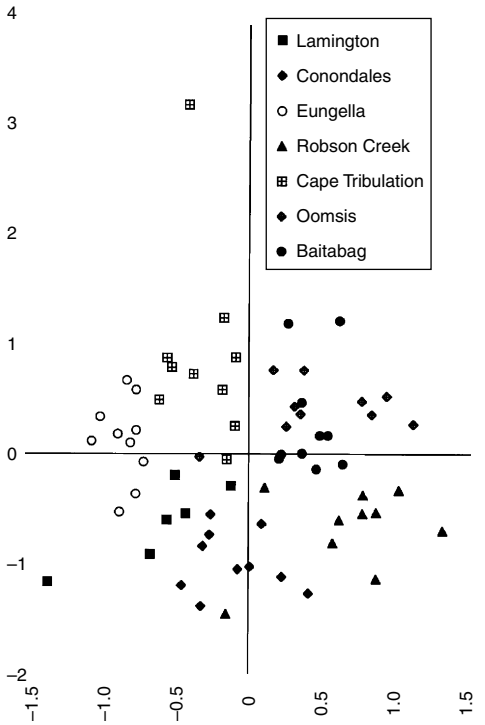

Figure 5 The ordination by multi-dimensional scaling of the results of the yellow pan trapping across study sites.

level of similarity at the assemblage level. The two subtropical sites are intermingled and clearly represent an explicable entity. The mid-elevation Atherton Tablelands site (Robson Creek) shows a greater similarity in these samples, with the subtropical sites, than it does with other Australian tropical sites. The wide scatter of the Eungella samples precludes any sensible interpretation within this sample.

Malaise trap samples

The ordination of the results of the Malaise trap samples are summarized in Fig. 4. The plot shows strong pattern with a stress value of 0.189. The ANOSIM analysis is highly significant ($P < 0.0001$). Each of the sites cluster clearly in a particular segment of the graph space except for the two subtropical sites, Lamington and the Conondales, which overlap substantially. The tropical sites occupy the top right-hand part of the space with no obvious further pattern. The Cape Tribulation samples (top left-hand corner) and the Oomsis samples (right hand, centre) are isolated from the remainder of the tropical sites.

These results support a very simple division between all the tropical sites (Eungella, Robson Creek, Cape Tribulation, Oomsis and Baitabag) and the two unequivocally subtropical sites (Conondales and Lamington). There is no clear pattern within the tropical sites (except for the left-hand outlying nature of the three Cape Tribulation samples). The Eungella sites are comprehensively mixed with the other tropical sites, yet separate from the subtropical sites.

Yellow pan samples

The results of the ordination of the data from the yellow pan traps is presented in Fig. 5. A stress value of 0.252 is again indicative of the large number of independent samples involved and the inevitable variability among them. The ANOSIM, nevertheless, produced highly significant results ($P < 0.0001$). The New Guinea sites clustered closely together in the top right-hand sector of the plot adjacent to the lowland Australian Cape Tribulation samples. The subtropical sites clustered adjacent to one another in the lower left-hand sector adjacent to the mid-elevation tropical site (Robson Creek) which clustered closely on the right-hand lower part of the plot. Unusually the Eungella samples plotted as a cohesive group on the left-hand margin of the graph.

These results are perhaps the most readily interpreted of any of the three sampling methods. The New Guinea sites cluster together very emphatically and sit adjacent to the lowland Australian results from Cape Tribulation. Similarly the subtropical sites are associated with each other intimately, and again the mid-elevation tropical results from Cape Tribulation are more similar to the subtropical ones than they are to the closest neighbouring site of Cape Tribulation. The Eungella sites are a separate entity and cluster between the lowland tropical and subtropical sites.

These multivariate results should be interpreted alongside the family-by-family ANOVAR results.

ANOVAR results

In general, results from the analyses of variance (Table 2) on levels of abundance parallel those on proportions. In this account we focus on the analyses of proportion but note those instances where analyses of simple abundances might produce different interpretations.

The analyses of Shannon diversity (H'), evenness (E) and richness (S) group together the subtropical sites with the mid-elevation, tropical Robson Creek site. This grouping extends to include the Eungella results for the evenness data. The analysis of the richness (S) data groups the Cape Tribulation results with one (but not both) of the New Guinea results. Values for Shannon diversity and evenness group the two New Guinea sites together and differentiate them from all Australian sites. The Shannon diversity measure obtained from the Eungella sample is significantly different from all others.

On a family-by-family basis there is a clear grouping of the two New Guinea sites with the lowland Australian site at Cape Tribulation for Muscidae and Tipulidae (in both cases these northern lowland sites had lower proportions of these families than other sites). When analyses of abundance (but not proportions) are considered the Dolichopodidae (higher levels) and Empididae (lower levels) are added to this grouping. A weaker grouping of the Cape Tribulation site with one, only, of two New Guinea sites is indicated for Chloropidae, Mycetophilidae and Empididae (all with lower proportions in these northern sites) where the Australian site linked with one but not both of the New Guinea sites. Again this weak linkage is evident, in addition, for the Cecidomyiidae when the analyses of abundance rather than proportion are examined. The two New Guinea sites grouped together (and differed significantly from the Cape Tribulation site) for the proportions of Dolichopodidae (where the New Guinea sites showed higher values) and the raw abundance of Muscidae, where lower numbers occurred in the two New Guinea sites.

There was clear evidence for a consistent subtropical grouping (of the Lamington and Conondales sites) for the Chloropidae Drosophilidae, Phoridae and Psychodidae (lower proportions), for the Mycetophilidae (a higher proportion), and for the Empididae (at an intermediate proportion). This unequivocal subtropical grouping was joined by the mid-elevation, tropical Robson Creek site for the Chloropidae and Phoridae. The Eungella results fell in with this grouping only in the case of the Chloropidae.

The isolation of the Eungella site from all others was evidenced by the results for the proportions of Empididae, Psychodidae and Tipulidae. In all three cases the proportions for these three families were significantly higher in the Eungella samples than in any other. The Chironomidae can be added to this list if the analyses of abundance are considered together with those on proportions.

DISCUSSION

The results of our study show that there are clearly interpretable if complex patterns in the taxonomic composition of dipteran assemblages from the seven sites surveyed. In interpreting these data there are two fundamental issues that need to be discussed. The first set of issues, crucial in any mixed method survey, are methodological; the second, relates to the underlying biogeographical patterns and the associated structuring mechanisms which generate and maintain the dipteran assemblages among and within sites. In addition, the ecological utility of targeting Diptera when sorted to the family level is discussed

Two general points need to be made at the outset. First, dipteran families may be very taxonomically and ecologically diverse (Hövemeyer, 2000). Accordingly where a family shows a prominence at, say, both a tropical and temperate site this may not be anomalous but simply a reflection of differential responses of different sections of the family. This bi- or multi-modal response is particularly likely in the very large families such as the Chironomidae, Phoridae and Cecidomyiidae. Secondly, we have established that the three trapping methods we have used target different segments of the dipteran fauna. This may well mean that particular sampling methods are targeting different taxa *within* a particular family – a further manifestation of the within-family diversity in many cases. These general issues must be borne in mind as we explore the processes underlying the patterns we observed. We return to this issue at the conclusion of our Discussion.

Methodological issues

Any arthropod-trapping protocol assumes that there is a set of objects (flies organized into recognizable families in our case) in the target area or areas about which we wish to know more. For the Diptera, ideally, we would like to know what families are present in the forest and in what relative proportions. In practise we are faced with two inevitable restrictions in our pursuit of this goal. First, any particular sampling method will target some taxa more efficiently than others and, indeed, may not capture some of the taxa at all. Secondly, we have to locate the traps that we use somewhere in the forest. We assume (with some confidence) that the flies we wish to sample are not dispersed randomly in the three-dimensional space that is the forest and, even if they were, we could not distribute our traps at random in that 3-space.

Accordingly, we make choices with respect to the type and style of trap we use and where we place them in the forest. We have demonstrated clearly that the three trapping methods we chose, target different but overlapping subsets of the dipteran fauna in all of our study sites. In the case of the canopy knockdown samples this is not too surprising given that it is the canopy fauna that is targeted by that method in spatial contrast to the other two. Both Malaise traps and yellow pan traps were set out at ground level. The clear differences in their catches reflect their method of operation. Malaise traps actively intercept insects that are flying (or, conceivably, being blown) past more or less parallel to the ground. In contrast yellow pan traps are collecting the mostly minute 'aerial plankton' which drifts down through the air within the forest or free-flying insects which are specifically attracted to the yellow colour or the reflective water surface of the traps.

We set out to use complimentary methods and our results suggest that we have achieved this goal. Other types of traps, or the same traps placed differently, however, would almost undoubtedly have produced different catch profiles. We deliberately avoided baited traps which are well known to target say fruit- or dung- or carrion-feeding species. Less comprehensive data sets that we have obtained using bark-spraying, or pitfall tapping, or litter extraction clearly target a different spectrum of dipteran families. We also observe that, for instance, Malaise traps erected in the canopy at some of our sites, may generate qualitatively and quantitatively different catches than do those erected at ground level (R. L. Kitching, unpublished observations).

Lastly the results we have obtained must be interpreted taking into account the overall size of our catches. In general, the Malaise traps caught about an order of magnitude more individual flies than did either of the other trapping methods. Inevitably therefore that method will catch more families as the large numbers that are examined reveal more and more of the entire fauna – another aspect of the well-known 'veil-line' problem (Magurran, 1988). In fact this will not bias the across-site analyses we have described as these have been carried out on a method-by-method basis. It must be borne in mind, however, when we compare different methods within sites and it is the reason that we have carried out few analyses on the rare families. They remain, of course, of considerable taxonomic interest.

Ecological patterns and processes

As has already been indicated the surveys discussed in this paper took place at different years although we attempted to match seasons across years as far as was practicable. The sites targeted were at different altitudes and inevitably reflected different geological substrates, histories and topography. Any pattern that we observe in the samples could reflect the uncontrolled effects of these and associated variables. To untangle the relative importance of the dozen or so environmental variables which we might use to characterize each site would require many more sites than we have or could reasonably be expected to have surveyed and, in any case, this was not the underlying purpose of the study. It is more productive to consider what the sites have in common. They were all broad-leaved (i.e. multi-species, non-coniferous, evergreen) forests with high tree diversity. They each showed few outward signs of human disturbance. Last, they all generated highly diverse samples presumably reflecting the underlying high diversity of the forests themselves.

In examining these results it is also significant that our very stringent statistical analyses generated, not just pair-wise site-to-site differences but multi-site patterns indicating that our choice of sites had captured 'real' underlying gradients. The explanation of these patterns is best approached using the standard fare of biogeography: ecological history and synoptic climate as mediated by latitude and altitude.

Biogeographical patterns and processes

Current Australasian rain forests contain combinations of the original Gondwanan flora with a history stretching back at least to the early Miocene. Elements of the Cunoniaceae (*Pseudowenmannia*, *Geissois*), Lauraceae (*Beilschmidtia*, *Cryptocarya*, *Endiandra*, *Litsea*), Myrtaceae (*Austromyrtus*, *Backhousia*, *Choricarpia*, *Pilidiostigma*, *Syzygium*) and Proteaceae (*Grevillea*, *Hicksbeachia*, *Macadamia*) are likely descendents of this original flora (Floyd, 1990). The docking of the so-called New Guinea Terranes of the South Caroline Arc of the Pacific plate with the northern edge of the Australian Plate some 5–15 Ma (Hall, 2001) established the huge continental island of New Guinea as we now know it. After this plate-to-plate contact Asian rain forest elements entered the Australian flora and are represented by families such as the Euphorbiaceae, Myristicaceae, Sterculiaceae, Meliaceae and Sapotaceae (note that these are families which have undergone substantial radiations in the Oriental region from whence elements invaded Australia: at an earlier time they may themselves have had Gondwanic ancestors). Basic family level distributions are illustrated in Heywood (1978). We have made surveys of all trees with stems greater than 5 cm d.b.h. at each of our 1-ha study sites (see Laidlaw, 1999; Laidlaw *et al.*, 2000, 2004; M. Laidlaw & R. L. Kitching, unpubl. data). A simple 'Gondwana Index' (GI) is arrived at by calculating the ratio of the number of genera in the dominant Gondwanic-radiated families (Cunoniaceae, Proteaceae, Lauraceae, Myrtaceae) to the number in the dominant Oriental-radiated families (Euphorbiaceae, Myristicaceae, Meliaceae, Sterculiaceae, Sapotaceae). Values for our sites from south to north are: Lamington 2.50, Conondales 1.44, Eungella 4.67, Robson Creek 1.29, Cape Tribulation 0.88, Oomsis 0.35 and Baitabag 0.21. Incidentally the value for a similarly surveyed site in Borneo, indisputably part of the Oriental region, is 0.49.

The advantage of taking this approach to characterizing each site is that it gets us away from the conventional but misleading 'subtropical' or 'tropical' descriptors. All our sites are broad-leaved, evergreen, diverse, closed forests yet the importance of their exact latitudinal position is confounded by altitude and by geological history. The balance between the original Gondwanic flora and the adventive Oriental elements captures the biogeography of the site in a biologically meaningful way. If we assume that the fauna has experienced similar biogeographical dynamics as has the flora then the 'Gondwanic Index' becomes a useful tool for interpreting faunistic patterns.

With this in mind we treat biogeographic issues by revisiting the three questions posed in the Results section, above.

The New Guinea connection

New Guinea is, currently, largely covered in mesic, rain forest vegetation but with extensive scleromorphic elements along the southern coastline. The modern island of New Guinea is characterized by a high central east–west cordillera (representing the likely consequence of the aforementioned tectonic 'docking'). Both of our New Guinean sampling sites are located north of this cordillera. New Guinea is currently separated from the Australian mainland by the 160 km stretch of Torres Strait (although this is dotted with the many islands of the Strait). The closest segment of the Australian mainland is Cape York peninsula which has, along its eastern coastline, a sequence of rain forest remnants and, at its base, the extensive lowland rain forests of the Daintree Region, location of our Cape Tribulation sampling site. New Guinea and Australia have been connected by land-bridges during glacial maxima several times over the last 2 Myr; most recently a mere 15–20,000 years ago. The nature of the vegetation cover during this period is less certain but it is likely that there have been times when more extensive moist forests have been present through the linking terrain.

The lowland forests that we have studied in New Guinea show the relatively greater importance of Oriental elements in their tree flora and share with the lowland forest of Cape Tribulation the distinction of having a preponderance of Oriental genera within the target plant families in our GI (values 0.21, 0.35 and 0.88 respectively). As expected the relative importance of the Oriental genera in the Australian, Cape Tribulation, site is less than in the New Guinean sites but the value of the index clearly aligns these three tropical sites together.

These considerations make an excellent rationale for any Australian/New Guinea faunal connections. Conversely, however, we know of many biogeographical connections which establish Oriental connections for New Guinea: the Dipterocarpaceae, woodpeckers and hornbills are cases in point. McAlpine (1982) indicates several such connections for the Diptera while suggesting that the Australian connections of the New Guinean acalyptrate dipteran fauna remain pre-eminent. The oriental connections may be the consequence of either deep time vicariance events or more recent dispersalist ones.

Our data present several points of support for the idea of a New Guinea connection, inasmuch as this will be reflected either by the dipteran fauna as a whole, or through specific families. For both the canopy knockdown data and the yellow pan data there is a clear multivariate adjacency of the New Guinean and Cape Tribulation data. Such a connection is not evident in the Malaise trap data. It is of interest that the two data sets which do show this association are unequivocally sampling different segments of the fauna – the mid-canopy on the one hand and the ground zone on the other. The catches from the Malaise traps, show significantly higher catches for 13 of the 14 common families, whereas knockdown and yellow

pan catches group together in six of 14 analyses of family abundance. Given that there is a significant site × method interaction for all 14 families analysed then the 'different' outcome for the Malaise traps in examining the New Guinea relationship is not surprising. The Muscidae and Tipulidae clearly emerge from our samples as subtropical or highland families isolating the New Guinea/Cape Tribulation grouping in a significant way (Table 2). The general interpretation of the Tipulidae, at least, as a more temperate family has been noted before (Alexander & Byers, 1981; Kitching & Theischinger, 1996). The two pre-eminent predatory families in our sample show interesting but contrasting results. The Dolichopodidae show significantly higher levels in the New Guinea/Cape Tribulation grouping, the Empididae show the reverse pattern. This is reflected in a higher species diversity of dolichopodids in the lowland tropical samples. Like the tipulids the Australasian empids in general also show a more southerly peak of diversity (D. Bickel, pers. comm.).

In only two cases was there evidence that associations existed between the two New Guinea sites to the exclusion of the Cape Tribulation sites. In both cases these are associated with results already discussed. The lower levels of abundance of Muscidae at the New Guinea sites reflect the low proportions already noted and which they share with the Cape Tribulation site. Similarly the significantly higher proportion of dolichopodids observed in the New Guinea sites reflects their higher absolute numbers (which they share with the Cape Tribulation site). We see no need to call upon additional explanations for these results over and above those already discussed.

The 'subtropical' fauna

During the Eocene the entire east coast of Australia probably comprised a strip of subtropical or warm temperate rain forest dominated by plant families such as the Proteaceae, Myrtaceae and Lauraceae together with the southern beech, *Nothofagus*. With the establishment of the circum polar current around Antarctica the southern regions of Australia cooled and the subtropical rain forest retreated northwards. Subsequently the forest fragmented with the distribution and size of fragments changing as ice-ages came and went from the late Miocene until the end of the Pleistocene. The mix of Gondwanic and Oriental flora that characterizes all Australian rain forests is also apparent in these more southerly sites. Current 'subtropical' rain forests contain combinations of the original Gondwanan flora with a history stretching back at least to the early Miocene (Floyd, 1990).

The values of the GI for both the Lamington and Conondales sites (latitudinally and, traditionally, undisputedly 'subtropical' in nature) show a preponderance of Gondwanic genera (index values of 2.50 and 1.44 respectively). However they share this characteristic with both the Eungella (GI = 4.67) and Robson Creek (GI = 1.29) sites. Both these more northerly sites are latitudinally tropical. The extreme values of the Eungella site will be discussed shortly. The Robson Creek site clearly shows floristic affinities that lie with the southerly subtropical sites rather than the much closer lowland tropical site at Cape Tribulation (see above).

These floristic results go a long way to help explain the patterns apparent in the Diptera data. The grouping of the Lamington and Conondales results within the ordinations is not in itself surprising and is characteristic of the data from all three methods. It is borne out by the family level analyses (see results) and could be explained using a naïve latitudinal explanation (similar latitude, altitude, climate and flora). In both the canopy knockdown and yellow pan results, however, these two southern sites cluster more closely with the Robson Creek sites then any other. This pattern is also clearly evident in analyses of the values for species richness, evenness and Shannon diversity. At the family level the connection of the two southerly sites with Robson Creek owes much to (lower levels of) Phoridae and Chloropidae.

The floristic analyses already discussed give support to the idea that these sites have experienced a similar history with the maintenance of strong 'southern' connections and perhaps a greater (perhaps climatically driven) resistance to invasion by the adventive northern elements. Of course, we are not trying to promote a causal connection between floristic composition and the composition of the dipteran assemblage: we suggest merely that the biogeographical factors which have produced the degree of 'mixing' of northern and southern elements so clearly supported by the botanical data may well have operated on the dipteran assemblages as well.

Eungella: a different place?

The rain forests of the Eungella massif are perhaps the most isolated of any in our set of study sites and represent one of the most isolated patches of this vegetation type in Australia. The Eungella Plateau west of Mackay rises to 1259 m at Mt Dalrymple adjacent to our study site. This is the highest point between the Bartle Frere/Bellenden Kerr Ranges of far northern Queensland (17° S, to 1622 m) and Mt Roberts on the Queensland/New South Wales border (28° S, 1381 m). The massif is probably Carboniferous comprising the volcanic intrusions of the so-called Urannah complex which, together with the Connors Volcanics, make up the Connors Arch of the southern Bowen Basin (Malone *et al.*, 1966). The rain forests of the Eungella plateau lie on the eastern part of the area and are mixed, evergreen forests ranging from complex lowland types in Finch Hatton Gorge to the much simpler notophyll forests of the high plateau. The GI (value 4.67) of these higher forests (where our site was located) shows that they have a very ancient vegetation with few northern adventives. The combination of the age of the forests, their isolation and elevation all contribute to a biogeographic uniqueness which is evidenced by endemic vertebrates and angiosperms (Winter & McDonald, 1986; Pearson & Pearson, 1992). Accordingly the special features within the Diptera data set which isolate Eungella from other sites are not surprising. The pre-eminence of the Empididae, Psychodidae, Chironomidae and Tipulidae in the Eungella assemblages suggests that these groups would be

worthy of further investigation using finer levels of taxonomic analyses. The cool climatic preferences of at least some of the Tipulidae, Chironomidae and Empididae have already been discussed and this is consistent with their significantly higher proportions in the high elevation Eungella samples.

Diptera as targets for biodiversity analysis

We echo the plea of Didham (1998) and Hurtado Guerrero *et al.* (2003) that more attention be paid to the Diptera in analyses of arthropod biodiversity. In this connection we make several inter-connected points. The results we present here include, we suggest, interesting, biogeographically interpretable patterns which at least complement those generated using other arthropod groups. The preponderance of a few readily recognizable families in our mass samples will make the task of sorting future samples for ecological purposes much less daunting (although noting that the target families would need to be defined afresh for studies of contrasting ecosystems). Many of the families which our analyses suggest are the most important in biodiversity analyses of rain forests are so called 'orphan taxa', at least within the Australasian region. For several of the largest families there is simply *no* taxonomic expertise available to analyse the fauna further. In an Australasian context this is true for the Phoridae, Sciaridae, Chloropidae, Mycetophilidae and Sphaeroceridae. Further there is little immediate prospect of this situation changing in the near future. We can only commend these groups to those who set training and, in particular, funding priorities.

We note, also, that all of these families are large and taxonomically diverse. We are proposing biogeographical explanations for patterns which emerge at the family level (in our analyses). We are, of course, aware that at best the patterns we observe and the explanations we offer will pertain to part of each family only – albeit a numerically dominant part. More precise interpretations will require sorting and analysis to finer taxonomic levels plus an understanding of the phylogeographic history of each family or part thereof. We are pursuing such analyses for those families for which appropriate expertise is available.

We conclude by noting that analyses at the level of the family, as we have demonstrated, provide robust and interesting quantitative bases for the generation of hypotheses at large geographical scales. Other authors have criticized the use of 'higher' taxonomic groupings in ecological analyses especially in the assessment of environmental quality in freshwater systems (Guerold, 2000; Lenat & Resh, 2001). Yet, in contrast, Krell (2004) provides a robust if conservative critique of the use of sorting to approximate species' equivalents ('morphospecies', 'parataxonomic units') which, in taxonomically poorly known regions and groups, is the unavoidable consequence of 'insisting' upon infra-familial levels of resolution in sorting of large biodiversity samples. Fundamentally those who presume to look for pattern in insect biodiversity operate in an information-imperfect world. Utility is the ultimate arbiter of methodological decisions on sampling protocols. Our results based on family-level data have increased *our* understanding of dipteran biogeography and will inform future work.

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