

# Diversity, distribution and community composition of Empididae, Hybotidae and Brachystomatidae (Insecta: Diptera) in Thailand - how did they arise?

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**Abstract** - Current knowledge of Empididae, Hybotidae and Brachystomatidae (Insecta: Diptera) in Thailand is summarized and likely diversity estimated. Currently 131 species are known but the total fauna is estimated to be 328–825 species. Rich communities are associated with many biotopes but moist evergreen forests are especially diverse. Biogeographic affinities at generic level and community-level distribution of taxa along environmental gradients (habitat, ecological characters, seasonality, altitude, etc.) are combined with endemism mapping and parsimony analysis of endemism to infer how empidoid communities might have responded to historical environmental changes. A General Historical Model of empidoid communities in Thailand is presented in which (i) the onset of the monsoon cycle forced altitudinal migration of “rainforest” biota to higher elevations where seasonality was relaxed and moist conditions prevailed throughout the year, (ii) orogenesis promoted speciation as mountain ranges became higher and more isolated, (iii) developing mountain chains provided continuity and immigration “corridors” effectively connecting Thailand’s mountains with others further north and south and (iv) oscillating climatic conditions, especially during recent glacial periods, caused repeated changes in sea-level and expansion and contraction of lowland seasonal forests encouraging migration from north and south.

**Keywords:** Biogeography, diversity, abundance, Empidoidea.

## 1. Introduction

Based on described species, the superfamily Empidoidea represents about 7.8% of world diversity of Diptera with 11,839 known species in about 400 genera (Yang *et al.*, 2006; 2007) and is distributed in all faunal realms except Antarctica. The systematics of Empidoidea have not been entirely resolved but the phylogenetic analysis of Sinclair and Cumming (2006) suggest that the superfamily is comprised of five families; Dolichopodidae, Empididae, Hybotidae, Atelestidae and Brachystomatidae. Atelestidae is a small family not known to occur in Thailand and although Dolichopodidae are undoubtedly highly speciose and abundant there, they were excluded from this account. The remaining families, Empididae, Hybotidae and Brachystomatidae (hereafter referred to as ‘Empidoidea’) are a conspicuous and often abundant part of the fly fauna in Thailand despite their small size (<1–10mm) and occur from sea level to the summit of the highest mountains at 2,500 m. So far as is known, all species are predatory in the larval stages (Steyskal and Knutson, 1981). Some are terrestrial, feeding on invertebrates within soils, dead wood, putrefying matter, etc., while others are aquatic or semi-aquatic found in both lotic and lentic environments and water saturated soils (Plant, 2011; Sinclair, 2008). Adults

are also predators; some genera catching prey during aerial pursuit flights but others have terrestrial habits hunting prey on leaf surfaces, tree-trunks or the ground. Nectar or more rarely pollen-feeding at flowers is present in some taxa (Cumming and Sinclair, 2009) and they may be important pollinators in some biotopes (Plant, 1994; Lefebvre *et al.*, 2014). Adults of the Empididae subfamily Empidinae are well known for their aerial epigamic courtship swarming behaviour involving secondary sexual ornamentation and transfer of nuptial gifts and are of great interest to understanding the evolution of behaviour and mate-selection theory (LeBas *et al.*, 2003; Bussière *et al.* 2008; Daugeron *et al.*, 2011a).

Recent intensive sampling and taxonomic analysis are leading to a better understanding of Empididae, Hybotidae and Brachystomatidae in Thailand (Plant *et al.*, 2011). The present work summarises current knowledge of their taxonomy, diversity, distribution and abundance and discusses aspects of their community structure, ecology and biogeography. It is based, in part on an oral presentation delivered by the author at the 8<sup>th</sup> International Congress of Dipterology, Potsdam, Germany in August 2014 (Plant, 2014).

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## 2. Taxonomic diversity

Thailand undoubtedly has a great diversity of ‘Empidoidea’. Although specimens of Empididae and Hybotidae are frequent in collections from Thailand (Papp *et al.*, 2006) only 23 described species of Empididae and 32 Hybotidae were listed by Yang *et al.*, (2007) and Brachystomatidae have only recently been detected (Plant, 2008; 2010). In attempting to properly delineate taxa occurring in Thailand, the taxonomist is hindered by a lack of comprehensive or regional systematic revisionary work for all but a few genera (noted below). Additionally, many empidid and hybotid genera are extremely speciose both within and beyond Southeast Asia with systematists reluctant to work on isolated and probably unrepresentative parts of a very large fauna. Despite this, for some genera, all the species known from Thailand have been described from short-duration sampling at single localities and it is extremely unlikely that the described species reported by such studies reflect overall diversity in the country.

Recent large-scale sampling efforts in Thailand (reviewed in part by Plant *et al.*, 2011) have made >50,000 specimens available for taxonomic study resulting in an accelerated rate of species-level recording and description although many more taxa certainly await discovery. Sampling effort has been biased towards the north and west of the country with the south, Central Plane and Isaan Plateau in the east being relatively less investigated. Published records of *described* species are available from 64 localities and their distribution and frequency reflects this sampling bias (Fig. 1). Currently 21 genera of Hybotidae, 12 Empididae and 2 Brachystomatidae are known from Thailand (Plant *et al.*, 2011) and the total number of described species is 131. Table 1 summarises current knowledge of the taxonomic diversity of ‘Empidoidea’ using recent and historical data and speculates as to likely total diversity based on examination of the large number of specimens present in recent collections. It is clear that many species remain to be described and the lower and upper limits of likely species richness of 328 and 825, respectively, are merely informed estimates that need to be refined by future detailed taxonomic studies.

**Table 1.** Diversity of Empididae, Hybotidae and Brachystomatidae in Thailand. The number of described species recorded (n) and the likely minimum – maximum range for the total number thought likely to occur (N) is given for each genus. Where a genus is known to be present but no described species have been recognized, its presence is indicated (\*).

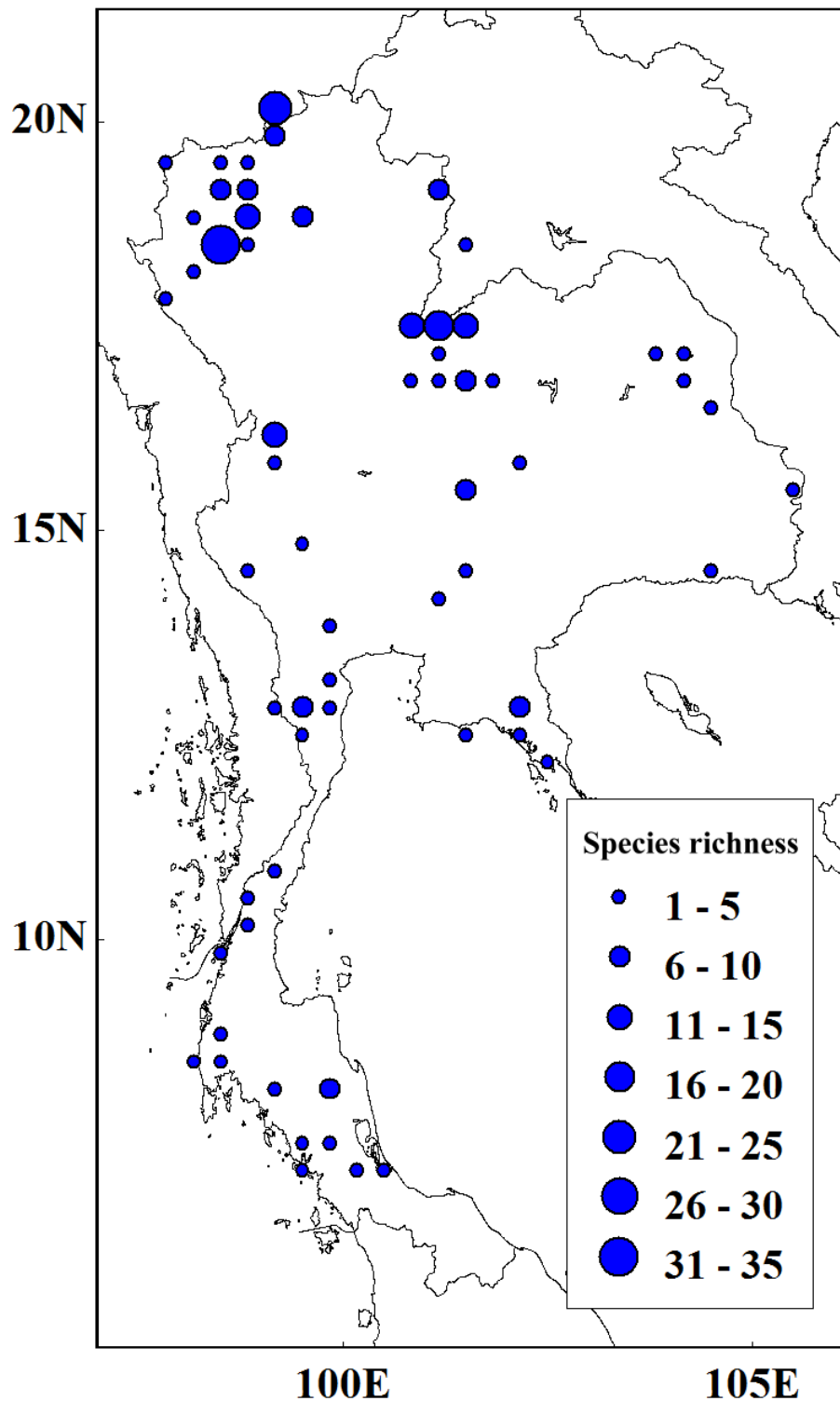
Family	Subfamily	Genus	n	N	Family	Subfamily	Genus	n	N
Empididae	Empidinae	<i>Empis</i>	16	30-50	Hybotidae	Hybotinae	<i>Chillcotomyia</i>	*	5-20
		<i>Hilara</i>	6	15-30			<i>Euhybus</i>	*	5-15
		<i>Rhamphomyia</i>	1	5-15			<i>Hybos</i>	41	50-75
	Hemerodromiinae	<i>Achelipoda</i>	3	4-6			<i>Syndyas</i>	*	8-20
		<i>Chelifera</i>	2	3-5			<i>Syneches</i>	*	8-10
		<i>Chelipoda</i>	14	18-25			<i>Bicellaria</i>	1	1-3
		<i>Phyllodromia</i>	*	1-2		Tachydromiinae	<i>Chersodromia</i>	2	4-10
		<i>Hemerodromia</i>	*	15-30			<i>Crossopalpus</i>	1	15-20
	Clinocerinae	<i>Clinocera</i>	*	2-5			<i>Drapetis</i>	*	10-25
		<i>Dolichocephala</i>	*	3-5			<i>Elaphropeza</i>	1	40-250
Brachystomatidae	Brachystomatinae	<i>Brachystoma</i>	1	1-2			<i>Megagrapha</i>	*	1-3
	Trichopezinae	<i>Trichopeza</i>	2	3-4			<i>Nanodromia</i>	4	8-15
							<i>Platypalpus</i>	10	40-70
Incertae sedis		<i>Hormopeza</i>	*	1-2			<i>Pontodromia</i>	*	2-8
							<i>Stilpon</i>	15	30-100
Hybotidae	Ocydromiinae	<i>Ocydromia</i>	*	2-5			<i>Tachypeza</i>	*	4-12
		<i>Leptopeza</i>	*	1-3			<i>Tachydromia</i>	9	15-20
	Oedaleinae	<i>Anthalia</i>	2	3-5					
		<i>Oedalea</i>	*	3-3					
		<i>Euthyneura</i>	*	1-3					

A summary of taxonomic diversity of ‘Empidoidea’ in Thailand will now be presented and biogeographic

affinities of the fauna discussed. Higher taxonomic classification is that of Sinclair and Cumming (2006)

**2.1 Empididae.** The three subfamilies of Empididae; Empidinae, Hemerodromiinae and Clinocerinae, are all represented in Thailand. The genus *Hormopeza* Zetterstedt, 1838 is present but its systematic position is not understood

and it is currently regarded as *incertae sedis* in Empididae (Sinclair and Cumming, 2006). In Thailand it is known from only one high-elevation locality in Chiang Mai Province and is probably genuinely very rare.



**Figure 1.** Map showing the distribution of described species of 'Empidoidea' in Thailand reported in the literature. Species richness is proportional to the size of the symbols.

**2.1.1 Empidinae.** Empidinae are predominantly flies of temperate forests and mountains and have radiated in both northern and southern hemispheres but are rather poorly represented in the tropics (Plant, 2011). The three genera known from Thailand – *Empis* Linnaeus, 1758; *Hilara* Meigen, 1822 and *Rhamphomyia* Meigen, 1822 are mega-diverse on a global scale (Yang *et al.* 2007) and taxonomically challenging (Bickel, 2009). *Empis* has a surprisingly rich fauna of 16 species (Daugeron and Grootaert, 2005; Daugeron *et al.* 2011) in Thailand. All but one of these belong to the predominantly oriental *Empis* (*Coptophlebia*) *hyalea* species-group and more species likely await discovery. The remaining *Empis* species is assigned to the *Empis* (*Coptophlebia*) *hyalipennis*-group which is conjectured to have originated in the Oriental tropics but is probably not speciose in Thailand. *Rhamphomyia* is known from a single Thai species (Barták and Kubík, 2008) belonging to the subgenus *Pararhamphomyia* Frey, 1922 and is the southernmost representative of the *ciliatopoda*-group. Other, presumably undescribed species of *Rhamphomyia* occur in Thailand but the genus does not appear to be species rich there. Only species of *Hilara* have been described from Thailand (Grootaert and Kiatsoonthorn, 2001; Shamshev and Grootaert, 2004), all from Loei Province, although the genus is certainly more widespread in the North and West. In temperate latitudes, *Hilara* is a conspicuous part of the empidid fauna, forming distinctive epigamic and feeding swarms over water (Plant, 2004). Similar behaviour in Thailand has been noted occasionally by the present author, with swarms usually forming close over fast flowing streams in shaded biotopes. It is improbable that such conspicuous swarming activity has been missed and the genus is unlikely to be diverse in Thailand.

**2.1.2 Hemerodromiinae.** Six out of 18 extent genera of this subfamily have been reported in Thailand (Plant *et al.*, 2012a). The tribe Hemerodromiini, in which the immature stages are strictly aquatic (Plant, 2011) living in usually well-oxygenated water, is represented by *Hemerodromia* Meigen, 1822 with many undescribed species, and by *Chelifera* Macquart, 1823 with two species (Horvat, 2002). *Chelifera* is essentially confined to the northern hemisphere with centres of diversity highest in the mountains of Western Europe and the Himalaya (Plant *et al.*, 2012a). Only species are known from China and its occurrence in Thailand at high elevation in the north suggests that it is at the extreme south-eastern edge of its range there. *Hemerodromia* is a speciose genus probably of recent origin in Eurasia (Plant *et al.* 2012) but there are many undescribed species especially in the tropical Neotropics (Câmara *et al.*, 2014) and insular Southeast Asia which Plant (2011) considered to be an undisclosed centre of diversity of the genus. In the absence of a formal phylogenetic analysis, it is unwise to speculate further on its biogeographic affinities.

Genera assigned to the tribe Chelipodini have immature stages associated with wet edaphic conditions (Plant, 2011) and inhabit moist soils in shaded biotopes.

*Chelipoda* Macquart, 1823 is represented by 14 described species in Thailand (Plant, 2009) but more probably await discovery, especially in forests in the west and south of the country. Taxonomy of the genus is imperfectly understood and a cladistic analysis by Plant (2011) revealed little evidence of its origin, with the Thailand species recovered in a poorly supported clade of almost world-wide distribution, excluding only the New Zealand Region. *Anaclastotecton* Plant, 2010 occurs from Nepal, through Southeast Asia and into eastern Australia with two species described from Thailand (Plant, 2010a). Considering its modern distribution and ‘basal’ origin in a clade with numerous Austral forms as sister-group, the genus may have had a southern temperate origin, migrating northwards into Asia during the Tertiary (Plant, 2010a; 2011). *Achelipoda* Yang, Zhang and Zhang, 2007 has three species in Thailand (Plant, 2009a). The genus has a tropical East Asian distribution with species recorded from Indonesia, Singapore, Vietnam as well as Thailand and there are undescribed species from China (D. Yang, *pers. com.*) and Japan (T. Saigusa, *pers. com.*). At least one species conforming with the generic diagnosis of *Phyllostromia* Zetterstedt, 1837 is present in Thailand (Plant *et al.*, 2011) but the validity of the genus has been questioned (Plant, 2011) and Asian representatives of the genus might be referable to *Chelipoda*.

**2.1.3 Clinocerinae.** Only two genera are known from Thailand, *Clinocera* Meigen, 1803 and *Dolichocephala* Macquart, 1823 but the species have not been delineated. The immature stages of clinocerines are aquatic occurring in water bodies, damp seepages etc (Sinclair, 2008). *Dolichocephala* seems to be madicolus and more or less confined to headwater streams and seepages in Thailand where it is probably not very diverse although sometimes abundant. The similarly depauperate fauna of *Clinocera* may be more strongly associated with flowing streams and sometimes, water-saturated soils in dense forest. Both genera have almost world-wide distributions (Sinclair, 1995).

**2.2 Hybotidae.** Four subfamilies of Hybotidae occur in Thailand. The Hybotinae is most diverse in tropical and subtropical regions of the Oriental and Neotropical realms (Chvála, 1983) whereas the mega-diverse Tachydromiinae have a world-wide distribution. Ocydromiinae have a predominantly Holarctic distribution (Chvála, 1983) but there are also many less well known genera in the southern hemisphere (Sinclair and Cumming, 2000). Only three genera of Oedaleinae are known from Thailand

**2.2.1 Hybotinae.** The genera *Chillcottomyia* Saigusa, 1986; *Euhybus* Coquillett, 1895; *Syndyas* Loew, 1857 and *Syneches* Walker, 1852 appear to be moderately species rich in Thailand but the included species have not been delineated. *Hybos* Meigen, 1803 has been intensively studied with 41 species currently recognised (Plant, 2013) distributed throughout the country. It has clear Oriental affinities and some species occurring in Thailand have wider distributions across eastern Asia whereas others

appear to be endemic to the country. *Bicellaria* Macquart, 1823 is a mostly Holarctic genus and the single species reported from Thailand, where it is restricted to high-elevation sites in the north, is the only Oriental representative (Barták *et al.*, 2013).

**2.2.2 Ocydromiinae.** *Ocydromia* Meigen, 1820 is present in Thailand but rather uncommon in trap samples and probably not very species-rich in the country. Although Papp *et al.* (2006) reported *Leptopeza* Macquart, 1827, the present author has not seen any examples of it in the large number of samples examined and the genus must be very rare in Thailand.

**2.2.3 Oedaleinae.** The essentially saproxylic *Oedalea* Meigen, 1820 and *Euthyneura* Macquart, 1836 are present in Thailand but the included species have not been evaluated. *Anthalia* Zetterstedt, 1838 is represented by two species (Grootaert and Shamshev, 2009). All oedaleine genera are considered unlikely to be species-rich in the country.

**2.2.4 Tachydromiinae.** This subfamily of minute to small flies is very species-rich in Thailand and while the genera *Drapetis* Meigen, 1822; *Megagrapha* Melander, 1928; *Pontodromia* Grootaert, 1994 and *Tachypeza* Meigen, 1830 are present, none of their representative species have been identified or described. *Platypalpus* Macquart, 1827 is known from just 10 species (Grootaert and Shamshev, 2006) from limited sampling effort in Loei Province, but more species await description, especially in evergreen forest biotopes of the northern mountains. This large genus is best known from the Palearctic but most of its included species-groups also occur in the Oriental where they show some preference for higher altitudes. All known Thai species belong to the tropical *P. albisetia*-group which in the Oriental realm is more species-rich in the south. *Elaphropeza* Macquart, 1827 is particularly speciose in the tropics and subtropics where a great diversity of similar species may indicate recent active radiation (Chvála, 1975).

Shamshev and Grootaert (2007) recognised two species-groups of *Elaphropeza*, a monophyletic *E. biuncinata*-group confined to the tropics and a less well defined *E. ephippiata*-group more widely distributed. Species conforming to both species-groups are present in Thailand but currently only a single widespread Southeast Asian species has been identified. In Singapore, Shamshev and Grootaert (2007) found 52 species of *Elaphropeza*, only four of which had been described elsewhere previously and the genus is undoubtedly also very speciose in Thailand, especially in the lowlands (Plant *et al.*, 2011). *Crossopalpus* Bigot, 1857 has one species and *Chersodromia* Haliday in Walker, 1851 has two (Grootaert and Shamshev, 2012) and are considered unlikely to be especially speciose, whereas *Stilpon* Loew, 1859 with 15 named Thai species (Shamshev and Grootaert, 2004a) is certainly very diverse there. *Nanodromia* Grootaert, 1994 with four Thai species (Grootaert and Shamshev, 2003) is a southern element of the 'Empidoidea' sharing with *Pontodromia* a centre of distribution in Papua New Guinea. Finally, *Tachydromia* Meigen, 1803 is likely moderately speciose in Thailand with species currently known (Shamshev and Grootaert, 2008).

**2.3 Brachystomatidae.** Two subfamilies of brachystomatids occur in Thailand, Trichopezinae which is restricted to the Palearctic and Oriental realms with two species of *Trichopeza* Rondani, 1856 recorded in Thailand (Plant, 2008) and the essentially northern hemisphere Brachystomatinae with just one species of *Brachystoma* Meigen, 1822 (Plant, 2010).

### 3. Distribution

Table 2 summarises geographical variation in abundance of Empididae and Hybotidae in Thailand. Both Hybotidae and Empididae occur throughout Thailand but overall, Hybotidae are the most abundant accounting for 74.6% of 18,675 specimens collected from 1,142 Malaise and pan trap samples from 33 national parks across the country analysed

**Table 2.** Regional variation in abundance of Empididae and Hybotidae. The percentage of Empididae and Hybotidae trapped in different is given; n = number of specimens in each region, nSpec = total number of specimens, nTrap = number of trapping events, nSite = number of trapping locations;  $R_h$  = trapping rate (number of specimens / trap event) for Hybotidae,  $R_e$  = trapping rate for Empididae. For details of sampling protocols and definitions of regional boundaries see Plant *et al.* (2011).

Region	Hybotidae		Empididae		nSpec	nTrap	nSite	$R_h$	$R_e$
	%	n	%	n					
Costal- Peninsula	99.7	380	0.3	1	381	28	1	13.57	0.03
East	90.5	804	9.5	84	888	167	12	4.81	0.50
North	75.0	7,888	25.0	2,630	10,518	489	8	16.13	5.38
Northeast	57.6	686	42.4	506	1,192	111	5	6.18	4.56
South	81.4	780	18.6	178	958	121	2	6.45	1.47
Southeast	80.0	72	20.0	18	90	34	1	2.11	0.53
West	71.8	3,333	28.2	1,306	4,639	192	4	17.36	6.80



by Plant *et al.* (2011). Furthermore, Hybotidae were consistently more abundant than Empididae across all regions of Thailand (Table 2). Amongst Hybotidae the subfamily Tachydromiinae predominates accounting for example for 79.8% of all hybotids in the North, 95.4% in the East and 93.0% in the South. Empidinae were the most abundant subfamily of Empididae, comprising 47.9% of all empidids in the North and were especially prevalent in the East (84.5%) but were proportionally less abundant in the South (19.7%) and West (21.5%). The empidid subfamilies Hemerodromiinae and Clinocerinae were rare or absent in the East and coastal areas of peninsular Thailand. Caution is needed in quantitative interpretation of trap data as both Malaise trap and pan trap catches are notoriously influenced by the interplay of trap design and positioning with the behaviour and ecology of the insects they catch (e.g. Muirhead-Thompson, 1991). While it is clear that both hybotids and empidids are widespread in Thailand, a proper analysis of distributions will require knowledge of the species and genera involved and of their habitat associations. It is becoming increasingly clear, for example (see below) that Empidoidea communities are profoundly shaped by the availability of aseasonal relatively moist habitats *versus* strongly seasonally arid habitats; correlations of taxon-ranges with the distribution of these habitats may be more informative than simple geographical distribution.

#### 4. Community structure

Understanding of community structure and composition of 'Empidoidea' in Thailand is severely limited by imperfect taxonomic knowledge of the species occurring there. Species-level (Plant *et al.*, 2012a) and genus-level (Plant *et al.*, 2011) investigations of how taxon composition of assemblages changes along altitude and seasonality gradients have been reported from two mountains in Chiang Mai Province, northern Thailand, while Plant *et al.* (2011) also provided an analysis of subfamily-level community composition of 15,553 specimens collected by 179 standardised trapping events throughout the country (summarised in Fig. 2).

Although Empidoidea occur at all altitudes in Thailand, they are generally least abundant at lower elevations. For example, in clusters A, B, C and D (Fig. 2) which represent mostly low altitude communities, the mean number of specimens in each sample ( $A^*$ ) varied from 1.4–58.0. At mid to high elevations (e.g. clusters E, F, H and I), values of  $A^*$  were typically higher (130–1,187). Most subfamilies are present to varying degrees at all elevations in Thailand. Notable exceptions are the Trichopezinae and Brachystomatinae which are entirely confined to higher mountains (where they are strictly associated with hill evergreen forest), and Clinocerinae which are most prevalent in moist hill evergreen forest above 2,000m (e.g. cluster F in Fig. 2). Clinocerinae are a minor component of the empidoid fauna at mid- and low-elevations and have a lower altitude threshold at ~400m below which they are not found (Plant *et al.* 2011). Hemerodromiinae can be significant components of some communities (e.g. clusters E and H), especially at mid-to high-elevations where both Chelipodini and Hemerodromiini occur. Non-metric multidimensional scaling and

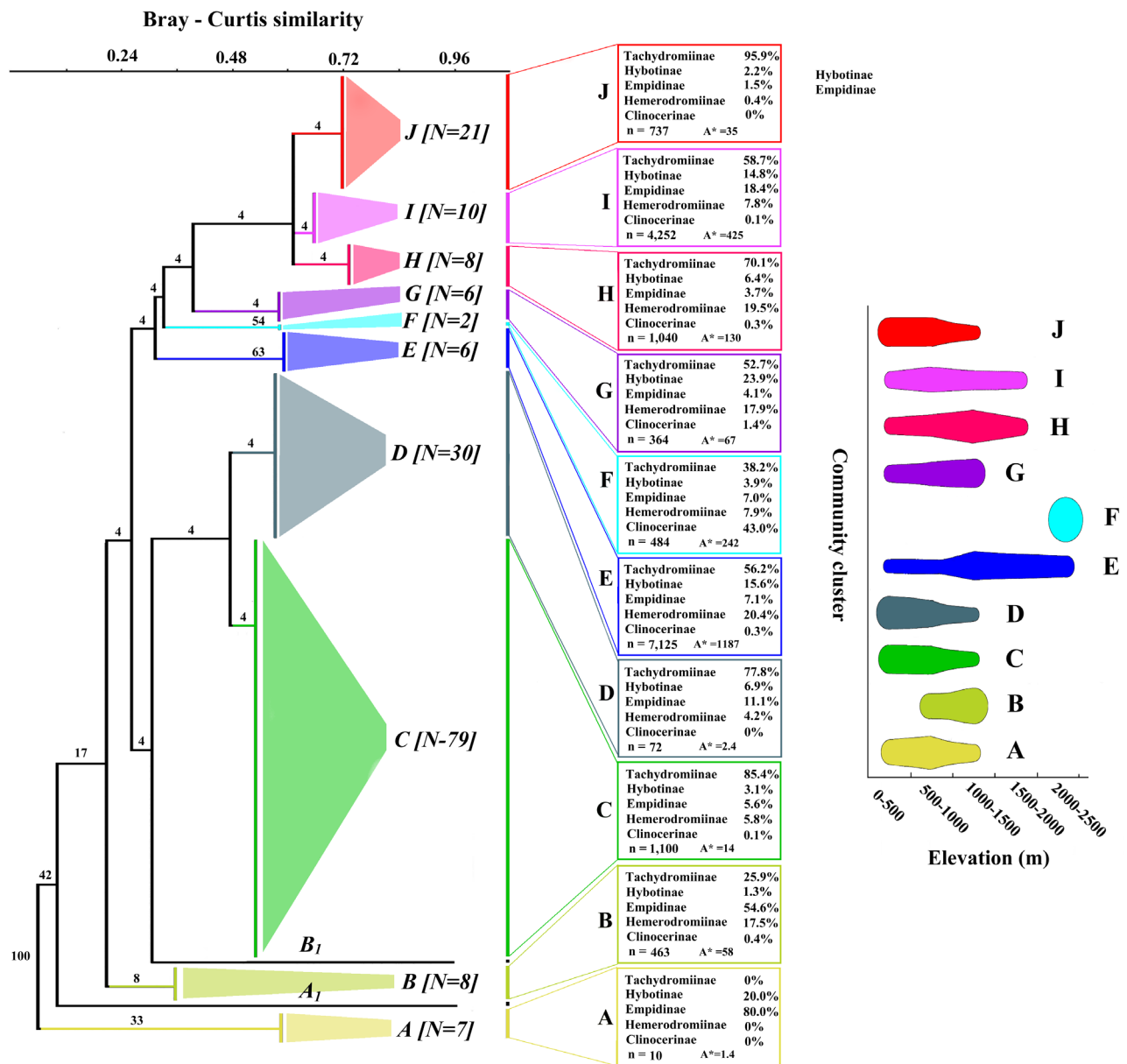
cluster analysis of species level associations of Hemerodromiinae on the mountain Doi Inthanon retrieved good support for a reasonably well defined and rich assemblage of species associated with the upper continuum of moist hill evergreen forest above 2,200m (Plant *et al.* 2012a). Chelipodini are strongly dependent on moist forest biotopes and become less prevalent in more seasonally arid biotopes at lower elevations whereas Hemerodromiini are strictly aquatic and occur even at low altitude where they are found in strict association with permanent flowing water in rivers and streams.

Empidinae were a relatively minor component of most subfamily assemblages revealed by cluster analysis. They were however dominant in cluster B (54.6% of all specimens) and especially cluster A (80%). By cross-referencing phenology and location of the samples in cluster B, it is apparent that it is associated largely with dry evergreen and lower hill evergreen forests at or below 1,500m, mostly in the North and West, and that peak capture rates were from December to March during the cool season. Similarly, cluster A represents mostly mixed deciduous, dry evergreen and other seasonally arid biotopes in predominantly northern and eastern localities and with adult emergence more or less restricted to the period from August to October in the latter part of the rainy season. Cluster I is also relatively enriched with Empidinae (18.4%) and occurs in dry evergreen and hill evergreen forests of the North and West.

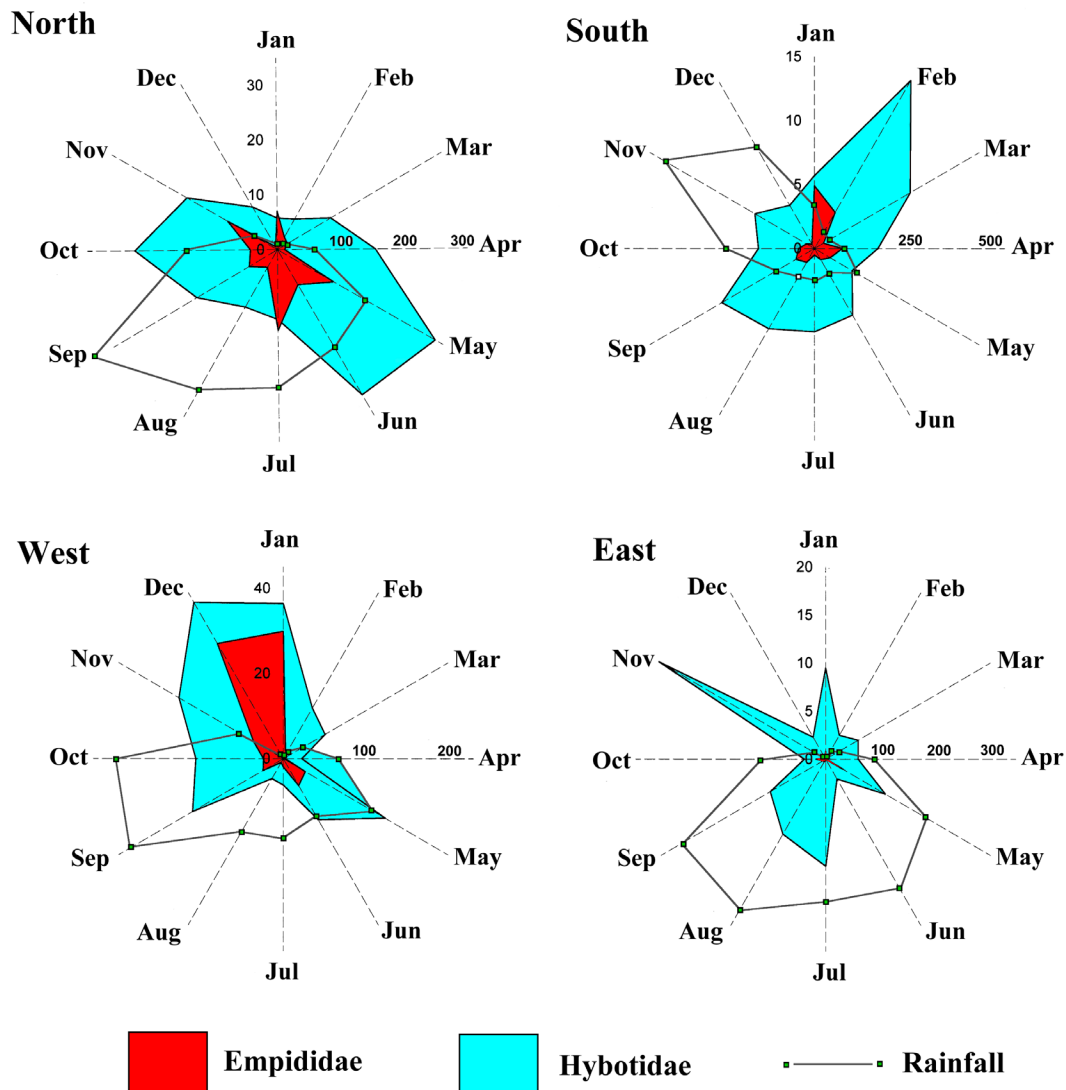
The hybotid subfamily Hybotinae was a significant element of clusters A (20.0%), E (15.6%) and I (14.8%) and was mostly constituted by species of *Hybos* (other hybotine genera being relatively rare). While a few widespread cosmopolitan species of *Hybos* are known from Thailand, diversity is greatest in mid to high elevation evergreen forests but lower in deciduous and dry Dipterocarp forests (Plant, 2013). Tachydromiinae are clearly a significant element of many 'Empidoidea' assemblages and were completely absent only in cluster A (Fig. 2). The tachydromiine tribe Drapetini (including especially *Elaphropeza*) appears to be most numerous in lowland seasonally arid biotopes whereas in higher elevation evergreen forest Tachydromiini (especially *Platypalpus*) predominates.

#### 5. Seasonality

Abundance of adult Empididae and Hybotidae changes throughout the year and varies across different regions of Thailand (Fig. 3). In northern Thailand abundance of hybotids was bimodal with maxima between September and November and in May and June whereas in the West a major peak of abundance occurred from November to January with a lesser peak in May. In the East abundance was greatest in July and November. In these regions, abundance is thus approximately correlated with the start and end (North), end (West) and middle (East) of the Southwest Monsoon and abundance is lowest during the hot, dry season between February and April. Southern Thailand also experiences the Northeast Monsoon and there abundance was also correlated with the start and end of the wettest period. In all regions, monthly abundance of Empididae approximately mirrored that of Hybotidae.



**Figure 2.** Cluster analysis of elevational relationships of subfamilies of Empididae and Hybotidae (excluding Oedaleinae, Bicellariini and Ocydromiinae which are very minor components of the fauna) from standardised 7-day Malaise trap captures at localities throughout Thailand using unweighted pair-group average and Bray-Curtis similarity indices. Bootstrapping was performed with 1,000 resamples and the percentage of replicates where each of the major clusters is still supported is shown as nodes. Major clusters are designated A, B, C, D, E, F, G, H, I and J (minor clusters A<sub>1</sub> and B<sub>1</sub> were each composed of a single terminus). The number of termini retrieved for each major cluster (not shown for clarity) is indicated by *N* and the percentage proportions of each subfamily present in each cluster is indicated in the box (*n* = number of specimens and *A\** = mean number of specimens/sample in each cluster). The comparative abundance of specimens across the elevation range of 0–2,500 m is shown schematically at the right. Adapted with permission from Plant *et al.* (2011).

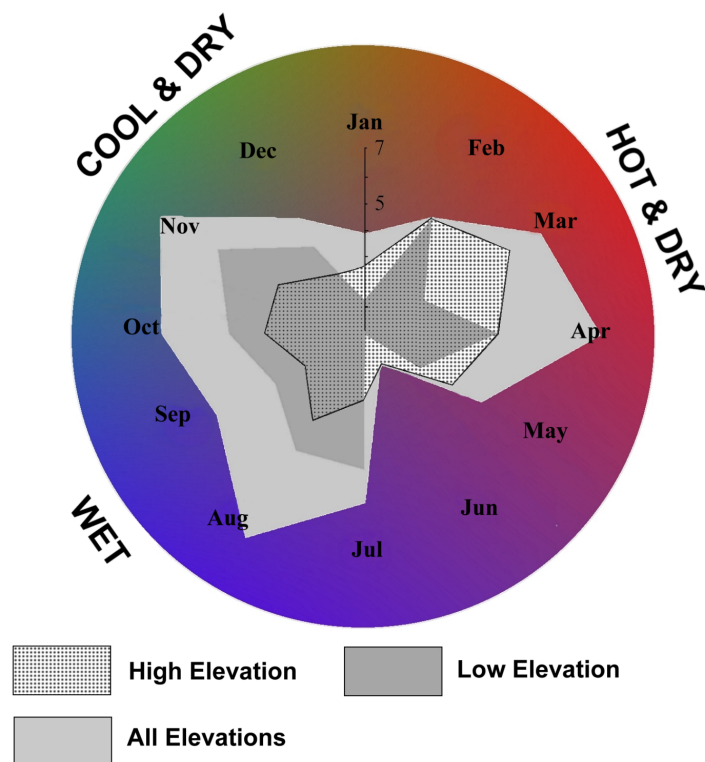


**Figure 3.** Radial plots of monthly variation in rainfall and abundance of Empididae and Hybotidae from standardised 7-day Malaise trap captures at localities throughout Thailand. Monthly abundance as mean number of individuals / trap-event in plotted on the January axis. Total number of trap events was 419 (North), 155 (West), 108 (South) and 76 (East). Rainfall as monthly average (mm) is indicated on the April axis using data from Chiang Mai (North), Kanchanaburi (West), Ubon Ratchatani (East) and Nakhon Di Thammarat (South). Adapted with permission from Plant *et al.* (2011).

As noted in Section 4, certain subfamily-level assemblages retrieved by cluster analysis, had phenologies linking them to wet phases of the monsoon cycle. In a study of ‘Empidoidea’ phenology on the mountain Doi Chiangdao in northern Thailand, Plant *et al.* (2011) reported that different genera correlated in different ways with rainfall patterns. Abundance of *Empis* for example was strongly associated with the onset of the monsoon whereas *Platypalpus*, *Elaphropeza*, *Hybos*, *Chelipoda* and *Achelipoda* were more persistent throughout the rainy season. Emergence of *Hybos* and *Achelipoda* was correlated with precipitation during the same month while *Elaphropeza* and *Platypalpus* were better correlated with the previous three month’s rainfall. Phenology of *Stilpon* and *Anaclastoctedon* were not obviously associated with

cycles of precipitation. On Doi Inthanon, species richness of *Chelipoda* was bimodal with the major peak of diversity between August and November during the latter part of the rainy season and a lesser peak during March to May (Fig. 4). The decrease in species richness during March to May was proportionally much less at high elevation and considered probably to be related to relaxation of seasonal aridity at higher altitudes (Plant, 2009). While it is clear that in general, species richness and abundance of ‘Empidoidea’ are positively correlated with seasonal rainfall, the patterns of occurrence vary between taxa and can be influenced by elevational amelioration of rainfall regimes and presumably, other (un-investigated) abiotic factors such as temperature.





**Figure 4.** Radial plots of species richness (number of species) of *Chelipoda* on the mountain Doi Inthanon throughout the year. Data for low, high and all elevations are plotted and approximate limits of the major seasons indicated. Adapted with permission from Plant (2009).

## 6. Endemicity

The extent and patterns of endemicity exhibited by 'Empidoidea' in Thailand can only be properly assessed for taxa which have received modern revisions, but even then, the possibility of error remains as diversity may still be underestimated (Section 2). Additionally, lack of knowledge of the fauna of nearby countries can not preclude the possibility that species known from Thailand might yet be found elsewhere. For revised genera, the percentage of species endemic to Thailand (with total number occurring there in brackets) are- *Hybos* 83% (41), *Chelipoda* 64% (14), *Achelipoda* 50% (6), *Brachystoma* 100% (1), *Trichopeza* 50% (2), *Bicellaria* 100% (1), *Anaclastocedon* 100% (2) and the *Empis* (*Coptophlebia*) *hyalea* species-group 100% (15). These figures suggest that the empidoid fauna is rich in endemics at a national scale. Estimation of local-scale endemism is even more difficult but Plant (2014) mapped areas of elevated endemism of *Hybos* centred on the Daen Lao and Thanon Thongchai ranges in the North and to a lesser extent in southeast Thailand. Doi Inthanon in the Thanon Thongchai range was revealed as a diversity 'hot-spot' for *Chelipoda* by Plant (2009). Some groups are probably radiating rapidly in montane hot-spots of the north and west. *Hybos phahompokensis* Plant from the Daen Lao and *H. inthanonensis* Plant from the nearby Thanon Thongchai ranges are closely similar species separated from each other primarily by small differences

in the male terminalia. Similarly, small differences in genital morphology of *H. serratus* Yang and Yang on different mountains of the Daen Lao and on the Petchabun Range and of *H. khamfui* Plant on the Daen Lao, Thanon Thongchai and Tenasserim Hills might be indicative of nascent speciation occurring in different mountain populations (Plant, 2013). *Chelipoda nakropa* Plant exists in two morphotypes separated by altitude and seasonal phenology in the Thanon Thongchai (Plant, 2009); it too might be in the process of active speciation.

## 7. Origin of the 'Empidoidea' fauna of Thailand

From the summary of knowledge of 'Empidoidea' in Thailand presented in previous sections, it is hypothesised that the fundamental characteristics of the empidoid fauna can be understood in terms of patterns of historical migration, endemicity, altitudinal segregation and responses to seasonality.

**Migration.** The fauna contains elements that immigrated from the north of essentially Palaearctic or Sino-Japanese origins (*sensu* Holt *et al.*, 2013) as well as southern elements derived from south Oriental, Oceanian or Australian faunas. Many of the immigrant forms considered to have northern origins (e.g. *Chelifera*, *Bicellaria*, *Rhamphomyia* and *Hilara*) are predominantly associated with moist forests habitats, in the north and west of Thailand. More cosmopolitan 'core' Oriental taxa (e.g. some species

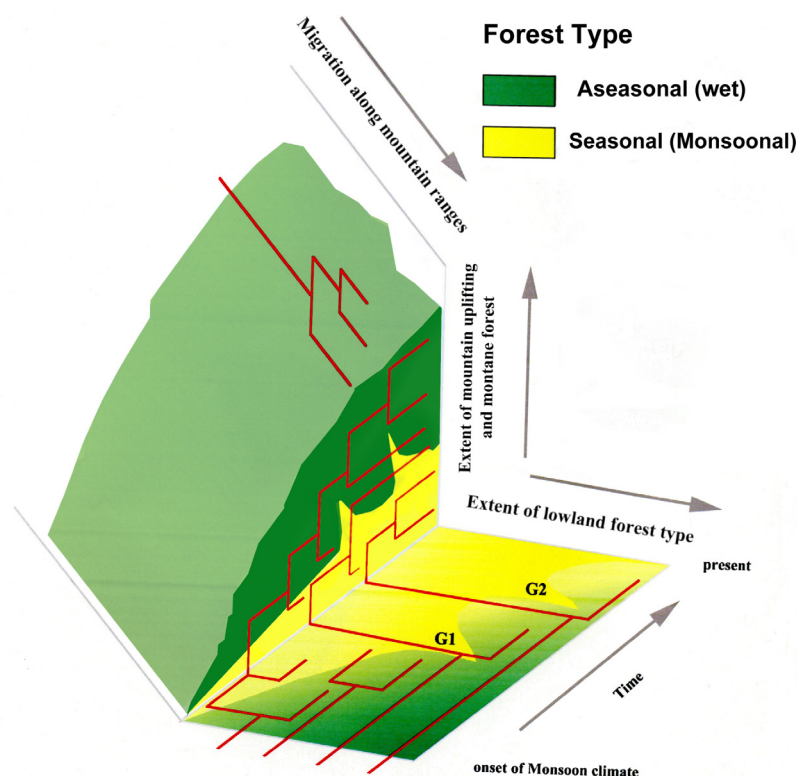
of *Hybos* and perhaps *Elahropeza*) and some thought to have arrived from the south (e.g. *Pontodromia* and *Nanodromia*) appear to be more prevalent in lowlands.

**Endemicity.** Certain areas, especially in the northern mountains appear to be hot-spots of diversity and endemism and may be active centres of radiation. Lowland-occurring Oriental taxa may be more widespread whereas montane elements with Palaearctic affinities may have more restricted distributions.

**Altitudinal segregation.** The fauna is particularly species rich, taxonomically diverse and abundant at mid to high elevations. At lower elevations, relatively drought intolerant Empididae (e.g. Clinocerinae and Hemerodromiinae) are less conspicuous whereas certain Hybotidae (e.g. some Tachydromiinae) may be proportionally better represented. Low elevation communities occur in deciduous, dry Dipterocarp and other seasonally water stressed biotopes whereas the richer mid to high elevation communities occur in less seasonally water stressed evergreen forests. Hill evergreen forests are particularly important to ‘Empidoidea’.

**Response to Seasonality.** For many taxa, abundance and diversity are strongly correlated with seasonality, usually being maximal during or at the start or end of the wet season. Seasonal correlations are weaker at higher elevations, an effect likely to be linked with relaxation of seasonal aridity in higher montane biotopes.

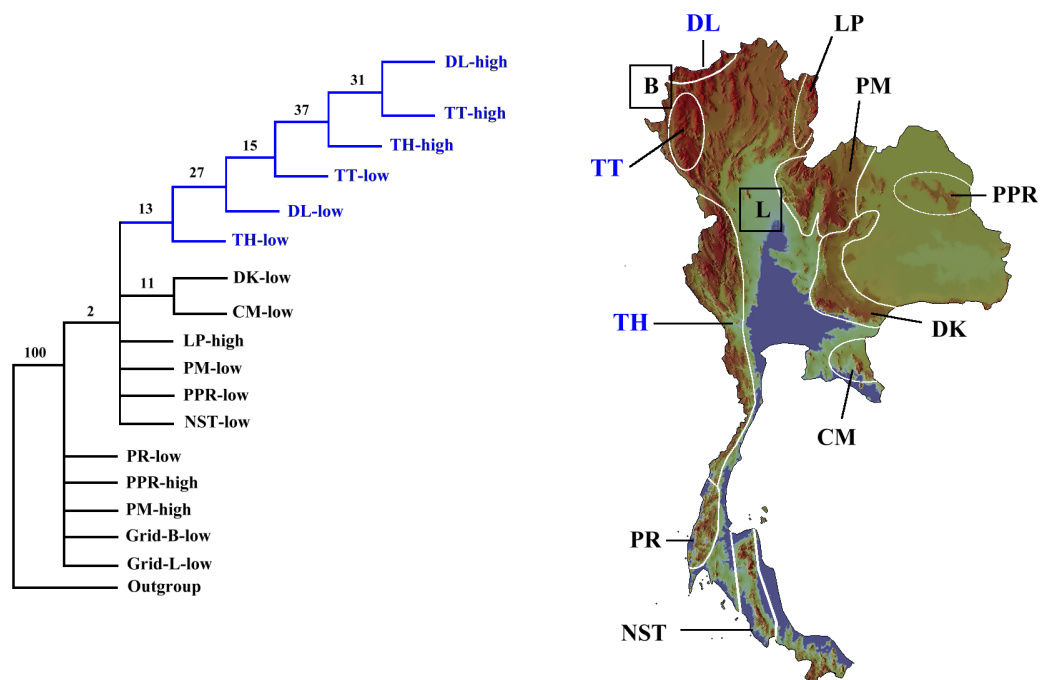
Uplifting of Thailand’s northern and axial mountains probably commenced following the collision of India with Eurasia ~50MYA (Royden *et al.* 2008), a process also responsible for the elevation of the Tibetan Plateau which initiated a seasonal monsoon climate perhaps as early as 15–20MYA (Harris, 2006). During the Miocene (10–23MYA) the climate of Southeast Asia was probably warmer with less seasonally dependant precipitation and tropical rainforests may have reached as far as Yunnan in southern China (Heaney, 1991; Zhu, 2008). During the Pleistocene, tropical forests retreated southwards in response to progressive climate cooling and modified rainfall regimes (Heaney, 1991; Penny, 2001; Voris, 2000) and montane vegetation and pine-grassland savannah became more prominent during glacial maxima (Heaney, 1991). Evidence from plants, mammals and palynological deposits indicate substantial migrations of Southeast Asian biota during this period in response to climatic drying and cooling (Penny, 2001; Werner, 1997; Canon and Manos, 2003). Amongst Diptera, Pleistocene environmental changes have profoundly influenced historical patterns of population fragmentation and survival in refugia followed by migration and recolonization in, for example, Culicidae (O’Loughlin *et al.* 2008; Morgan *et al.*, 2011) and Simuliidae (Pramual *et al.*, 2005; 2011; Paramual and Wongpakam, 2013).



**Figure 5.** Schematic illustrating Climate History Model of migration and radiation of ‘Empidoidea’ in Thailand. The horizontal plane of the figure shows how the proportion of seasonally dry (monsoonal) lowland forest has increased historically with ‘spikes’ of aridity during glacial maxima (G1 and G2). Concurrent uplifting of new mountain ranges (vertical plane) resulted in moist aseasonal montane forest into which taxa that failed to adapt to increasing aridity could migrate altitudinally and radiate. Connectivity with remote mountain ranges along mountain arcs provided ‘corridors’ of wet forest through which migration occurred from outside the region. Adapted with permission from Plant *et al.* (2012a).

A Climate History Model recently developed by Plant *et al.* (2012a) to explain current diversity patterns of Hemerodromiinae in Thailand may have wider applicability for understanding modern patterns of distribution of the wider biota of Thailand and Southeast Asia. The model reconciles understanding of historical migration, endemism, altitudinal segregation and responses to seasonality summarised in the present work, with the palaeoecological history of the region, and is entirely consistent with wider evidence that many taxa have historically responded to changing temperature and precipitation regimes by niche-tracking along environmental gradients (Graham and Grimm, 1990; Lyons, 2005; McCain and Colwell, 2011). The Climate History Model (shown schematically in Fig. 5) postulates that historically concurrent orogenesis of Thailand's mountain ranges, development of a seasonally arid monsoon climate and dry periods associated with glacial maxima, may have forced historical partitioning of moisture sensitive biota between seasonally dry lowlands into aseasonal moist forests in the highlands. As lowland biotopes became increasingly arid, taxa that were unable to adapt to the dryer conditions were either extirpated or forced to track the upward displacement of suitably moist niche-space. Subsequent radiation occurring on nascent mountains would have resulted in the new areas of speciation

becoming increasingly isolated, leading to increased endemism as mountain building continued, with montane populations becoming increasingly isolated by intervening seasonally arid lowlands. Support for past migrations along elevation gradients is provided by elevation zoned parsimony analysis of endemism for the genus *Hybos* in Thailand (Plant, 2014a) in which lowland area-clades in the northern and western mountains were recovered in positions ‘basal’ in respect of those at high elevation in the same geographical area (Fig. 6) suggesting that the high elevation fauna may have been derived historically from that at low elevation. Concomitant with the upward displacement of ancestral lowland ‘rainforest’ fauna, the expansion of low elevation seasonally arid biotopes, would have allowed for increased immigration of ‘core’ Oriental taxa in the lowlands and, especially during cool glacial maxima when sea levels were depressed considerably, facilitated immigration of southern elements into Thailand. The general pattern of decreasing connectivity of increasingly isolated mountains and increasing connectivity (if intermittent) of lowland habitats is consistent with the observation that Oriental ‘core’ taxa tend to be widely distributed in lowlands whereas those of supposed Palaearctic or other origin tend to be more restricted on mountains.



**Figure 6.** Elevation zoned parsimony analysis of endemism down-weighted against homoplasy using altitudinally zoned mountain ranges as operational geographic units and ‘characters’ made additive. Strict consensus tree of two equally parsimonious trees (CI = 0.716, RI = 0.534) produced by maximum parsimony analysis with weighted characters and TBR branch swapping in TNT (version 1.1.). Symmetrical resampling support is given under the nodes. Alphabetic codes of termini correspond with mountain ranges as follows. CM, Cardamom Mountains; DK, Dong Paya Yen – Khao Yai Forest Complex; DL, Daen Lao; LP, Luang Prabang; PM, Petchabun Mountains; PPR, Phu Pan Range; PR, Phuket range; TH, Tenasserim Hills; TT, Thanon Thongchai. B and L refer to grids of one degree of latitude and longitude that were not assigned to any mountain range. The suffixes ‘low’ and ‘high’ refer to low (<1,250m) and high (>1,250m) elevation sample data for each mountain range or grid. For detailed methodology see Plant (2014a). Adapted with permission.

While continuing orogenesis in combination with lowland aridification may have resulted in greater isolation of the different ranges *within* Thailand's axial mountains, at a larger scale the formation of mountain arcs linking them with the greater Himalaya to the northwest would have promoted greater connectivity with the Palaearctic. Areas of high elevation moist forests along mountain arcs might have functioned as 'corridors' allowing niche-tracking of Palaearctic elements such as *Rhamphomyia* and *Chelifera* into Thailand and of southern elements such as *Anaclastoctedon* to reach the eastern Himalaya.

## 8. Concluding remarks

Taxonomic knowledge of Empididae, Hybotidae and Brachystomatidae in Thailand remains in its infancy; the 131 described species known to be present perhaps representing as little as 16% of the total fauna likely to be found eventually. Significant efforts are underway to identify or describe the remaining 'Empidoidea' taxa but until such studies are substantially more advanced and supported, for example, by thorough phylogenetic and phylogeographic evaluations, a proper understanding of the distributions, ecology and origins of the fauna will remain elusive. It is however already apparent that Thailand has a rich empidoid fauna, with complex communities present in many different biotopes, and that the fauna has been assembled from geographically disparate origins by complex historical interplay of geography, climate and ecology.

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