

Areas of endemism in Thailand: has historical partitioning between seasonally dry lowland and aseasonal moist mountain forests shaped biodiversity in Southeast Asia?

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Abstract. Areas of endemism for the genus *Hybos* (Insecta: Diptera: Hybotidae) in Thailand were mapped as reciprocal weighted endemism at a resolution of 1° of latitude and longitude. Species richness and endemism were greatest in the northern and western mountains (Tenasserim Hills, Thanon Thongchai and Daen Lao ranges) and less so in south-eastern mountains (Cardamom Mountains and Dong Paya Yen – Khao Yai Forest Complex) but local hotspots of endemism were also evident within single mountain ranges. Understanding patterns of local invertebrate endemism, is considered important to identifying areas of conservation priority in Thailand. Parsimony Analysis of Endemism (PAE) recovered a ‘basal’ polytomy thought to reflect the presence of widespread lowland ancestral populations with Oriental affinities, from which more recently derived area clades were resolved representing contemporary populations in the northern, western and south-eastern mountains. When geographical areas were segregated according to altitude and analysed by PAE, area clades from low elevations of the northern and western ranges were recovered in positions ‘basal’ in respect to those at high elevations suggesting that the *Hybos* fauna at high elevations may have been derived historically from lower elevation fauna. It is argued that the results are consistent with a Climate History Model explaining diversity hotspots on the mountains as being, in part, a consequence of historical altitudinal partitioning between seasonal lowlands and aseasonal highlands in response to increasing aridity arising from development of a monsoon climate and Pleistocene climatic drying episodes.

Key words. biodiversity, biogeography, conservation, Diptera, Hybotidae, *Hybos*

INTRODUCTION

Thailand is situated within both the Indo-Burma and Sundaland biodiversity mega-hotspots identified by Myers et al. (2000) as globally significant. In the Indo-Burma hotspot, for example, species richness and percentage endemism respectively are estimated to be 13,500 (52%) for plants, 202 (56%) for amphibians, 484 (41%) for reptiles, 329 (22%) for mammals and 1170 (12%) for birds (Conservation International, 2013). In common with most, if not all tropical countries, knowledge of Thailand’s biodiversity is incomplete and is largely restricted to plants and vertebrates. Total invertebrate biodiversity cannot be reliably estimated at present and although Hutacharern et al. (2007) catalogued 10,191 species of insects and mites from Thailand, species richness is undoubtedly much higher (Plant et al., 2011). Patterns of distribution and local endemism in Thailand remain poorly studied, especially in invertebrates. The current lack of knowledge, especially at a smaller geographical scale, hampers its incorporation into conservation planning. Invertebrates constitute the majority of eukaryotic species and while they can be good surrogates of the diversity of plants

and vertebrates, the reverse is not true as the latter taxa are often poor at predicting the diversity of invertebrates (Moritz, et al., 2001). Endemism may be apparent at different spatial scales in different taxa (Platnick, 1991) and it is essential that invertebrate diversity and endemism be included in biodiversity assessments (Harvey, 2002; Brennan et al., 2004; Hamer et al., 2006) and considered at an appropriate scale.

Thailand’s rich and often unique biota has clearly been strongly shaped by historical migrations occasioned by changing sea-levels, Pleistocene glacial episodes, a developing monsoon cycle, and by persistence of relic populations in moist forest refugia during periods of climatic fluctuation (Jablonski, 1993; Plant, 2009; Pramual et al., 2005; Pramual & Wongpakam, 2013; Tougard, 2001; Werner, 1997). A Climate History Model recently developed by Plant et al. (2012) to explain current diversity patterns of the fly subfamily Hemerodromiinae (Diptera, Empididae) in Thailand may have wider applicability for understanding modern patterns of distribution of the wider biota of Thailand and mainland Southeast Asia. The model hypothesises that contemporary distributions have been profoundly shaped by historical responses of biota to climatic drying associated with glacial maxima or to increased seasonal aridity associated with the development of a seasonal monsoon climate. 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

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of moisture-sensitive biota between seasonally dry lowlands into aseasonal moist forests on highlands with subsequent radiation on nascent mountains. Furthermore, dispersal along corridors of montane moist forest may have facilitated interchange between Palaearctic and Oriental biotic elements and the spread of lowland seasonally dry biotopes would have allowed the dispersal of more drought tolerant species. The Model is a conjecture based largely on a comparison of palaeoclimatic and geological history with contemporary patterns of species richness, diversity, community structure and systematic relationships. It was developed for a group of highly moisture dependant taxa (some Hemerodromiinae have aquatic immature stages while others require moist edaphic conditions) and although it is consistent with the body of evidence demonstrating linkage between historical migrations and palaeoclimate mentioned above, it has not been formally tested, and its applicability to less moisture sensitive organisms is unclear.

The genus *Hybos* Mg. (Diptera: Hybotidae) is widely distributed with more than 200 described species, of which ~75% are confined to East and Southeast Asia with ranges embracing eastern parts of the Palaearctic and especially the Oriental realms (Plant, 2013). Adults inhabit a wide variety of moist and semi-arid biotopes and in Thailand are prominent constituents in some Empidoidea communities occurring from near sea level to the summit of the highest mountains at 2,500m (Plant et al., 2011). The immature stages remain little known but emergence trap data indicates that they inhabit soils (Delettre et al., 1998; Meyer & Filipinski, 1998) and some species at least, are clearly not associated with very moist edaphic conditions. A recent taxonomic revision has revealed at least 41 species occurring in Thailand (Plant, 2013) and provided detailed distribution data enabling areas of endemism for the genus to be investigated in the present work.

Parsimony Analysis of Endemism (PAE) is a method used to generate historical hypotheses of relationships between the biota of different geographical areas. PAE is analogous to cladistic methods used in phylogenetic analysis and classifies areas or Operative Geographical Units [OGU] (cf. taxa in cladistics) by their shared or synendemic taxa (cf. characters grouped by synapomorphies in cladistics) according to the most parsimonious solution. The method was originally developed from a dynamic perspective interpreting the distribution of taxa across two or more stratigraphic horizons (Rosen, 1988a; Rosen & Smith, 1988) but has been argued to also be applicable from a static perspective where distribution patterns are analysed from a single horizon (Rosen, 1988b). Although static PAE has been widely used (e.g., García-Barros et al., 2002; Linder, 2001; Navarro et al., 2007) its validity has not been universally accepted (e.g., Brooks & van Veller, 2003; Nihei, 2006). Rosen (1988b) has pointed out that in certain cases, static PAE may be considered tentatively as dynamic, namely where: (1) the recurrence of a particular pattern among several groups of organisms is a consequence of geological events, (2) a single PAE pattern can be used to construe an hypothesis about the history of areas when reconciled with geological evidence, and (3)

PAE cladograms are associated with and explained using palaeoecological data.

In this work, patterns of endemism of species of the genus *Hybos* in Thailand are mapped and then analysed by PAE. A modification of PAE is applied in which for each endemic area, OGU's are defined on the basis of altitude—high elevation and low elevation (Elevation Zoned Parsimony Analysis of Endemism – EZPAE)—in order to investigate the hypothesis that historical partitioning between lowland seasonally dry forests and highland aseasonal forests has contributed to modern patterns of diversity. It is argued that the observed partitioning is reconcilable with palaeoclimatic and palaeoecological data.

MATERIAL AND METHODS

Sampling. Material used in this study was mostly collected between 2004–2009 during three mass sampling projects throughout Thailand. Multiple Malaise traps were deployed for one year at multiple elevations in 33 national parks. The number of parks sampled in each region and approximate sampling density (as number of parks sampled 1000 km⁻² in each region) were: Northern region, 8, 0.099; North-eastern region, 5, 0.118; Eastern region, 12, 0.063; Western region, 4, 0.075; Central region, 1, 0.012; Southeast region, 1, 0.087 and Southern region, 2, 0.004. Trapping effort was not uniform across all national parks sampled as different numbers of traps were deployed in different parks. Sampling was not random but was based on the distribution of national parks and apparently 'suitable' habitat (=forest) within them. The Central region for example is largely under agriculture and has few national parks so was poorly sampled. Sample distribution was also constrained by the geography of Thailand which has a large land area in the north and much smaller area available for sampling in the southern peninsular region. For details of sampling effort, methods and locations see Plant et al. (2011, Fig. 1 and Table 1). Further material ($\leq 10\%$ of total) were collected by variable-duration Malaise trapping events at three localities in Chiang Mai Province between 2010–2012 and occasional fieldwork using hand-netting by the author, throughout Thailand from 2007–2012.

Species richness and endemism mapping. Species richness (number of species present in an Operational Geographic Unit [OGU]) using data for 2,146 specimens of 41 species of *Hybos* occurring in Thailand (Table 1) as detailed in Plant (2013), supplemented with two specimens from the Canadian National Collection, Ottawa, were mapped at a resolution of 1° of latitude and longitude using DMAP software (A. Morton, Windsor, UK). Because certain species occurring in Thailand have wider distribution ranges, overlapping into China and Vietnam for example, estimations of endemism also incorporated extralimital distribution data, extracted from the literature and summarised in Plant (2013). Using this combined data, endemism for each OGU was calculated as reciprocal weighted endemism, using a modification of the method of Moir et al. (2009) as follows: 1) The number of OGU's within which each species occurred was counted; 2) Each species was then assigned a value based on this

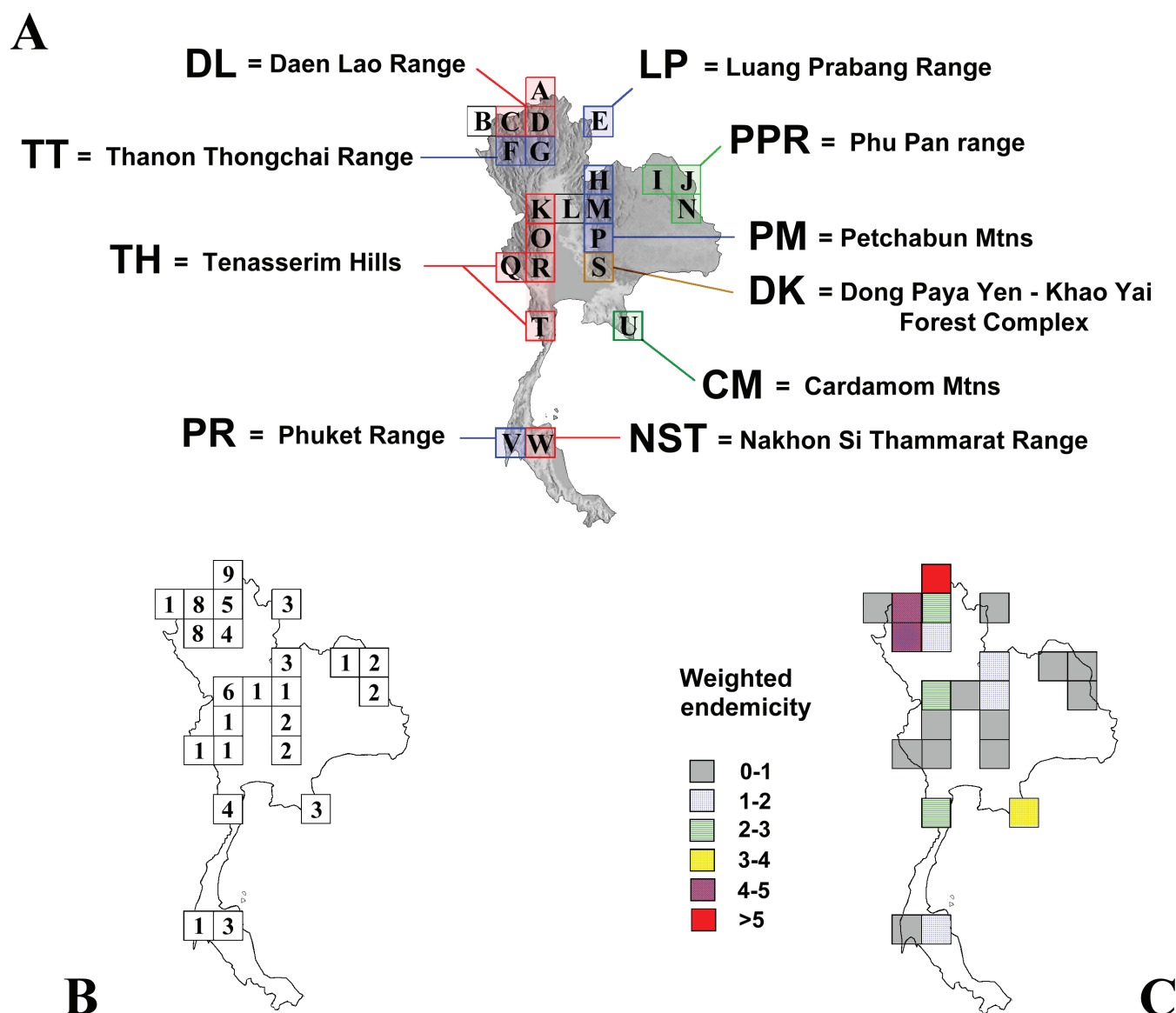


Fig. 1. Maps of Thailand showing: A, Grid of 1° of latitude and longitude denoted by single-letters A–W. Mountain ranges are indicated by two- or three letter codes (CD, DK, DL, LP, NST, PM, PPR, PR, TH & TT) and the grids that comprise each range are colour-coded. Grids B and L were not assigned to any mountain range; B, Species richness (number of species) of *Hybos* present in 1° grids; C, reciprocal weighted endemism of *Hybos* spp. calculated for 1° grids.

number with *Hybos* spp. known from only one OGU being given the highest value of 1, *Hybos* spp. occurring in two OGU's were given a value of 0.5, three OGU's valued at 0.333 and so forth; 3) Weighted endemism for each OGU was then calculated as the sum of values for each species whose range overlapped the OGU. Linear regression and the diversity parameter of Dominance ('D', 1-Simpson index) were calculated in PAST (Hammer et al., 2001).

Parsimony analysis of endemism. The data matrix used for Parsimony Analysis of Endemism (PAE) is given in Table 1 and that for Elevation-Zoned Parsimony Analysis of Endemism (EZPAE) in Table 2. PAE and EZPAE were performed using TNT v1.1 (Goloboff et al., 2008). The program was allocated sufficient memory to hold 10,000 trees and general RAM was set to 1,000 Mb. Traditional parsimony-based searches employed implicit enumeration where only a small number (<14) OGU's were involved, but otherwise employed 100 random-addition replicates

using tree bisection reconnection (TBR) branch swapping, retaining 10 trees per replication. Support was calculated by symmetrical resampling using 1000 replicates.

Traditional parsimony-based searches were performed with 'characters' uniformly weighted (prior-weighted) or down-weighted against homoplasy (which could be introduced by widespread species occurring partially in several areas of endemism and could result in those areas being obscured) using the protocols of Linder (2001).

An outgroup with an all-0 score (all species absent) was arbitrarily set up. PAE was performed using OGU's at two different spatial scales. Firstly, OGU's were defined as grids of 1° of latitude and longitude. Secondly, OGU's were defined as areas delimited by discrete mountain ranges. Selection of mountain ranges as OGU's can be justified as they are generally geographically distinct and represent discrete areas of endemism of Empidoidea in general (Plant

Table 1. Presence (+) or absence (-) of 41 spp. of Hybos in 23 Operational Geographical Units (OGU) comprised of 1° latitude and longitude grid squares. OGU's are indicated as A-W and their geographic location is given in Fig. 1A.

OGU	Taxon																							
	Outgroup	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W
<i>H. zhejiangensis</i> Yang & Yang, 1994	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. yungyak</i> Plant, 2013	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. xishuangbannaensis</i> Yang & Yang, 2004	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0	0	0
<i>H. tilokarati</i> Plant, 2013	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
<i>H. thepkaisoni</i> Plant, 2013	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. thaosao</i> Plant, 2013	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1
<i>H. tetricus</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>H. subapicalis</i> Plant, 2013	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. stigmaticus</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1
<i>H. steatopygus</i> Plant, 2013	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. songbai</i> Plant, 2013	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. sinclairi</i> Plant, 2013	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. shamshevi</i> Plant, 2013	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. serratus</i> Yang & Yang, 1992	0	1	1	1	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>H. saenmueangmai</i> Plant, 2013	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
<i>H. pisadaanus</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
<i>H. phahompokensis</i> Plant, 2013	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. particularis</i> Yang, Yang & Hu, 2002	0	0	0	1	0	1	0	1	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1
<i>H. paknok</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>H. ngachang</i> Plant, 2013	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. merzi</i> Plant, 2013	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. men</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>H. meeamnat</i> Plant, 2013	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. mangraii</i> Plant, 2013	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. longus</i> Yang & Yang, 2004	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. lannaensis</i> Plant, 2013	0	1	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. konkaogwang</i> Plant, 2013	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. khamfui</i> Plant, 2013	0	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. kaluang</i> Plant, 2013	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
<i>H. inthanonensis</i> Plant, 2013	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. hylobates</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>H. grootaerti</i> Plant, 2013	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. divisus</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>H. daugeroni</i> Plant, 2013	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1
<i>H. chaweewani</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
<i>H. bispinatus</i> Plant, 2013	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0
<i>H. apicichamatus</i> Yang & Yang, 1995	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. anisoserratus</i> Plant, 2013	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. ancyclochiles</i> Plant, 2013	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. ancistroides</i> Plant, 2013	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1
<i>H. aceriformis</i> Plant, 2013	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

Table 2. Matrix used in E/ZPAE showing absence (0), presence at <1,250m (1) or presence at >1,250m (2) of 41 spp. of *Hybos* in mountain ranges (abbreviated as CD, DK, DL, LP, NST, PM, PPK, PR, TH, & TT; see Fig. 1A for locations of ranges) and two 1° grid squares which were not assigned to a mountain range (see Fig. 1A for locations of grids). Within each mountain range operational geographical units (OGU) were defined for areas <1,250m (low) and >1,250m (high).

OGU	Taxon																										
		Outgroup	DL_high	DL_low	TT_high	TT_low	TH_high	TH_low	PR_high	PR_low	NST_high	NST_low	CM_high	CM_low	DK_high	DK_low	PRN_high	PRN_low	PM_high	PM_low	LP_high	LP_low	GridB_high	GridB_low	GridL_high	GridL_low	
	<i>H. zhejiangensis</i> Yang & Yang, 1994	0	0	2	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. yungyak</i> Plant, 2013	0	0	2	2	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. xishuangbannaensis</i> Yang & Yang, 2004	0	0	2	2	0	1	0	2	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	<i>H. tilokarati</i> Plant, 2013	0	0	2	2	0	0	2	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. thepkaisoni</i> Plant, 2013	0	0	2	2	0	0	0	2	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. thaosao</i> Plant, 2013	0	0	0	0	0	0	0	1	0	2	0	1	0	0	0	1	0	0	0	0	0	2	0	0	0	0
	<i>H. tetricus</i> Plant, 2013	0	0	2	0	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. subapicalis</i> Plant, 2013	0	0	2	0	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. stigmaticus</i> Plant, 2013	0	0	2	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
	<i>H. steatopygus</i> Plant, 2013	0	0	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. songbai</i> Plant, 2013	0	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. sinclairi</i> Plant, 2013	0	0	2	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. shamshevi</i> Plant, 2013	0	0	2	2	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. serratus</i> Yang & Yang, 1992	0	0	2	0	1	0	2	0	1	0	2	2	0	0	0	0	0	0	0	2	0	1	0	0	0	0
	<i>H. saenmueangmai</i> Plant, 2013	0	0	0	0	0	2	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. pisadaanus</i> Plant, 2013	0	0	0	0	0	0	0	2	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. phahompokensis</i> Plant, 2013	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. particularis</i> Yang, Yang & Hu, 2002	0	0	0	1	0	0	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
	<i>H. paknok</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	<i>H. ngachang</i> Plant, 2013	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. merzi</i> Plant, 2013	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. men</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. meeannat</i> Plant, 2013	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. mangraii</i> Plant, 2013	0	0	2	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
	<i>H. longus</i> Yang & Yang, 2004	0	0	2	2	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. lannaensis</i> Plant, 2013	0	0	2	2	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. konkaogwang</i> Plant, 2013	0	0	2	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. khamfui</i> Plant, 2013	0	0	2	2	1	2	2	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. kaluang</i> Plant, 2013	0	0	2	2	0	1	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. inthanonensis</i> Plant, 2013	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. hylobates</i> Plant, 2013	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. grootaerti</i> Plant, 2013	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. divisus</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	<i>H. daugeroni</i> Plant, 2013	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0
	<i>H. chaweewani</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. bispinatus</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. apicichamatus</i> Yang & Yang, 1995	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. anisoserratus</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. ancyclochiles</i> Plant, 2013	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0
	<i>H. ancistroides</i> Plant, 2013	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>H. aceriformis</i> Plant, 2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

et al. 2011) and *Hybos* in particular (Plant, 2013). Whereas in the first method, OGU's had identical surface areas, in the second method the area of OGU's was not constant as mountain ranges in Thailand have differing sizes and the OGU's defining them were selected to include a variable number of component 1° grids occurring within the area of the mountain range.

Each of the 23 1° grid squares in which species of *Hybos* were recorded was designated by letters A–W (Fig. 1A, Table 1). The assignments of grid squares to mountain ranges is indicated in Fig. 1A and were as follows: Cardamom Mountains – CM (= grid U); Dong Paya Yen-Khao Yai Forest Complex – DK (= grid S); Daen Lao Range – DL(= grids A, C, D); Luang Prabang Range –LP (= grid E); Nakhon Si Thammarat Range –NST (= grid W); Petchabun Mountains – PM (= grids H, M, P); Phuket Range – PR (= grid V); Phu Pan Range – PPR (= grids I, J, N); Tenasserim Hills – TH (= grids K, O, Q, R, T) and Thanon Thongchai Range – TT (= grids F, G). Grid squares B and L could not be readily assigned to any mountain range and each was treated as an OGU.

For EZPAE, OGU's were defined by areas occurring below or above an altitude threshold at 1,250m in each mountain range. A matrix was constructed (Table 2) in which data for each of the mountain ranges (Fig. 1) was segregated into that occurring below 1,250m (low) or above 1,250m (high); for example in the Thanon Thongchai Range (TT), one OGU includes all species occurring below 1,250m (TT-low) and another for species present above 1,250m (TT-high). OGU scores for ranges lacking physical geography or sample data for either above or below 1,250m were excluded from the analysis. In EZPAE analyses, the occurrence of a taxon in a lower elevation (<1,250m) OGU is scored as '1' whereas its presence in a high elevation (>1,250m) OGU was scored as '2' and 'characters' were either treated as random, or additive. The dividing threshold at 1,250m was selected because throughout much of Thailand, it approximately coincides (Plant et al., 2011) with the transition between lowland seasonally arid forest types (mixed deciduous, dry dipterocarp etc.) and less seasonal highland forest types (dry evergreen, hill evergreen etc.). However, it should be noted that this threshold is perhaps less useful in the wetter forests of the southern Peninsula and also that some forest types (e.g., *Pinus* forest) in the north substantially overlap the threshold elevation.

RESULTS AND DISCUSSION

Patterns of species richness and endemism. Species richness of *Hybos* throughout Thailand is generally greatest at mid-elevations (between 1,000 and 1,600m, data not shown) above which larger numbers of fewer species occur and dominance (D) declines (data not shown). The observation that species richness was clearly greatest in the mountainous areas of the north and west of Thailand (Fig. 1B) and lower in the south and east should consequently be treated with caution as the mountains of southern and eastern Thailand are commonly of lower elevation than those in the north and

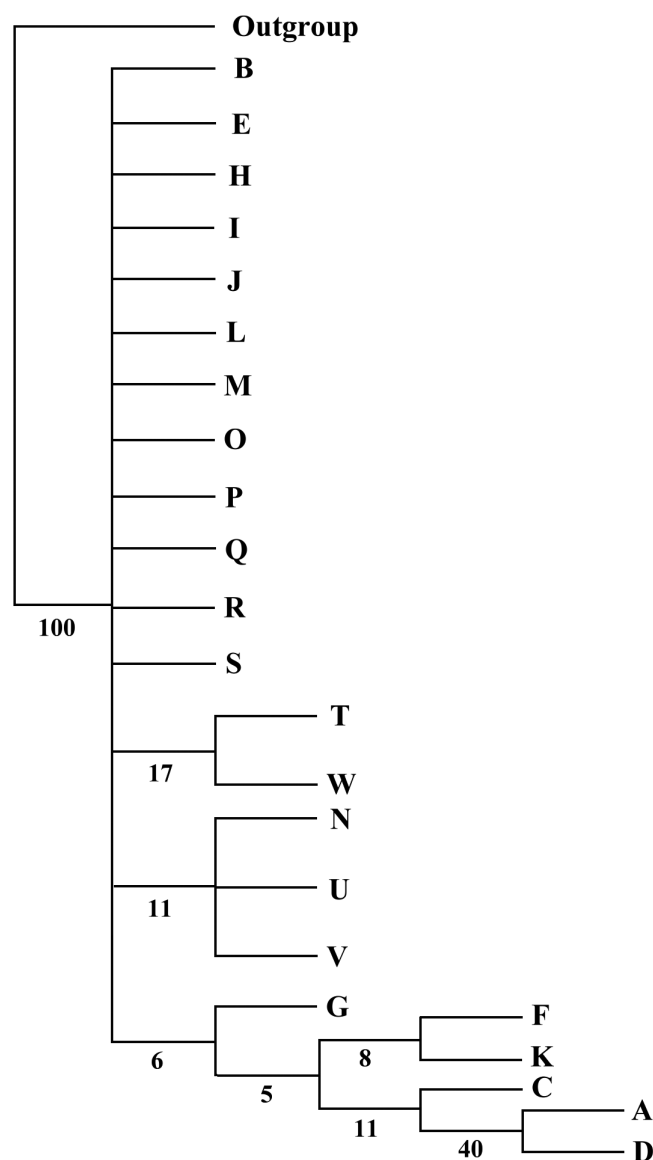


Fig. 2. PAE using 1° grids as OGU. Strict consensus tree of 760 equally parsimonious trees (CI = 0.501, RI = 0.557) produced by maximum parsimony analysis with unweighted 'characters' and TBR branch swapping in TNT. Symmetrical resampling support is given under the nodes (see Fig 1A for explanation of alphabetic codes).

west and fewer higher elevation samples were possible. Of 41 described species of *Hybos* occurring in Thailand, 33 (80%) are apparently endemic to the country. Local endemism is concentrated in the north and west, especially in the Daen Lao (DL = grids A+C+D) and Thanon Thongchai (TT = grids F+G) ranges and in the northern Tenasserim Hills (TH = grids K+O+Q+R+T) (Fig. 1C) but important areas of endemism were also found elsewhere, particularly in the Cardamom Mountains (CM = grid U) in the south-east and southern Tenasserim Hills around the base of the Thailand Peninsula. It is interesting that high levels of endemism occur not only in different geographically close mountain ranges but also that local endemism was evident within ranges. For example, the endemic fauna of the Daen Lao Mountains (grid squares A, C & D in Fig. 1A & 1C) differs from that of the nearby Thanon Thongchai Range (grid squares F & G) but within the Daen Lao range itself, grid squares A and C both constitute endemism hotspots (probably reflecting major

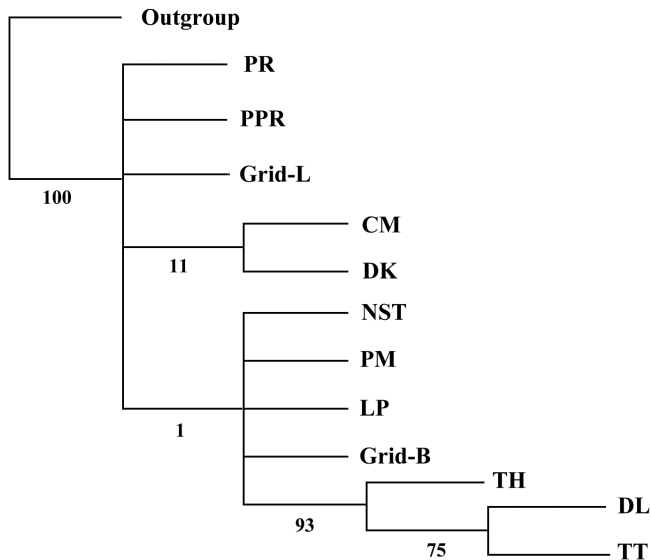


Fig. 3. PAE using mountain ranges as OGU. Strict consensus tree of nine equally parsimonious trees (CI = 0.745, RI = 0.722) produced by maximum parsimony analysis with weighted 'characters' and implicit enumeration in TNT. Symmetrical resampling support is given under the nodes. Abbreviations. – CM, Cardamom Mountains; DK, Dong Paya Yen – Khao Yai Forest Complex; DL, Daen Lao Range; LP, Luang Prabang Range; NST, Nakhon Si Thammarat Range; PM, Petchabun Mountains; PR, Phuket Range; PPR, Phu Pan Range; TH, Tenasserim Hills; TT, Thanon Thongchai Range. Grid-B and Grid-L refer to 1° grids (B and L in Fig. 1A) that were not assigned to any mountain range.

faunistic composition differences between two separate and more extensively sampled mountains within the range—Doi Phahompok and Doi Chiangdao, respectively). It would have been desirable to determine the patterns of local endemism at higher resolution than was possible here. However, proper assessment of the spatial scale of local endemism requires data to be sampled without the geographical biases discussed in the materials and methods section. Data also needs to be sufficiently dense to support the grid size (Laffan & Crisp, 2003) and in this study, the relative paucity and patchiness of data did not allow meaningful analyses with cells less than one degree. The detection of patterns of local endemism, even at this scale, is however an important contribution to identifying areas of conservation priority and to understanding local biogeography.

Historical origins of endemism. PAE using 1° grids of latitude and longitude as OGU returned a high level of polytomy (Fig. 2) from which only a group of northern grid squares (A, C, D, F, G, K) and two groups comprising southern and eastern grids (T, W & N, U, V) were resolved with weak support. When OGU's were selected by grouping 1° grids according to the mountain ranges they overlapped and PAE down-weighted for homoplasy, 'basal' polytomy was still apparent (Fig. 3) but the northern and western mountain ranges (Daen Lao, Thanon Thongchai & Tenasserim Hills) again resolved in a better supported terminal clade and two geographically close south-eastern ranges (Cardamom Mountains and Dong Paya Yen-Khao Yai Forest Complex) were recovered in a weakly supported clade.

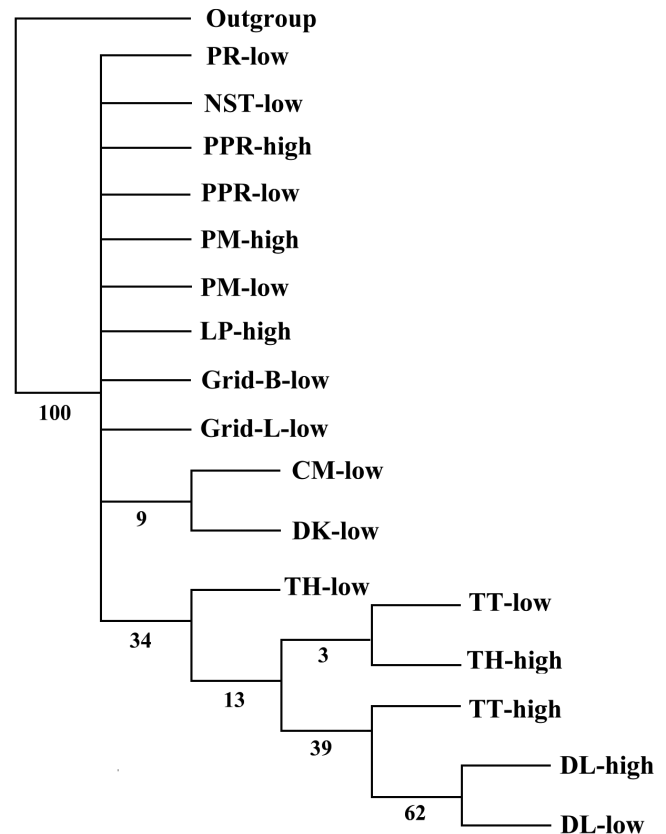


Fig. 4. EZPAE down-weighted against homoplasy, using altitudinally zoned mountain ranges as OGU, 'characters' made non-additive. Strict consensus tree of four equally parsimonious trees (CI = 0.674, 0.580) produced by maximum parsimony analysis with weighted 'characters' and TBR branch swapping in TNT. Symmetrical resampling support is given under the nodes. Alphabetic codes of termini correspond with mountain ranges as abbreviated in Fig. 3; the suffixes 'low' & 'high' refer to low (<1,250m) and high (>1,250m) sample data.

EZPAE down-weighted against homoplasy using low and high elevation areas of mountain ranges as OGU (Fig. 4) also recovered the northern and western mountain ranges in a more clearly resolved clade but with only weak support. The two south-eastern ranges also grouped together with poor support and all other OGU's were included in a 'basal' polytomy. However, when the same analysis was run using additive 'characters' (state 1 = <1,250m, state 2 = >1,250m) tree topology was similar (Fig. 5) but the 'basal' polytomy was broken by a very weakly supported group (clade-1 in Fig. 5) from which the northern and western ranges (clade-2) and the two south-eastern ranges (clade-3) were better resolved although symmetrical resampling support remained low.

Both PAE and EZPAE consistently resolved, albeit with weak support, two area clades substantially comprising (i) the northern and western mountains (Daen Lao & Thanon Thongchai ranges and the Tenasserim Hills) and (ii) the south-eastern ranges (Cardamom Mountains and Dong Paya Yen – Khao Yai Forrest Complex). These two mountainous areas appear to have experienced largely different histories from each other and from the remaining areas of the south, central and eastern Thailand which were generally poorly resolved in a 'basal' polytomy.

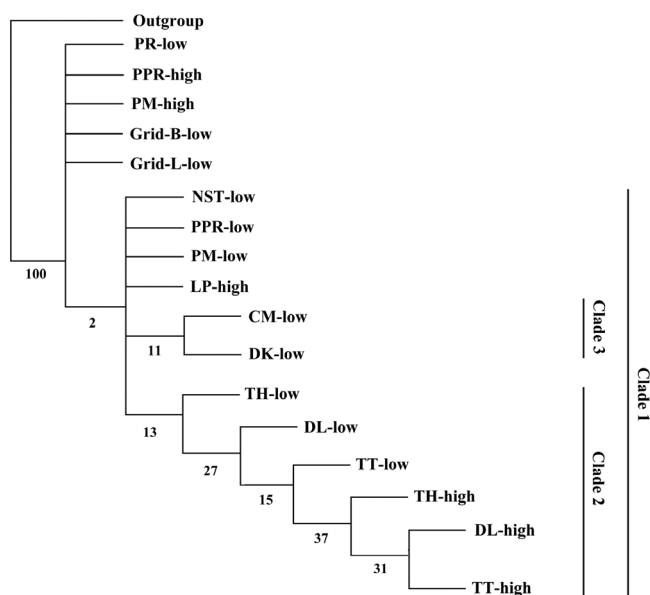


Fig. 5. EZPAE down-weighted against homoplasy, using altitudinally zoned mountain ranges as OGU, ‘characters’ made additive. Strict consensus tree of two equally parsimonious trees (CI = 0.716, RI = 0.534) produced by maximum parsimony analysis with weighted ‘characters’ and TBR branch swapping in TNT. Symmetrical resampling support is given under the nodes. Alphabetic codes of termini correspond with mountain ranges as abbreviated in Fig. 3; the suffixes ‘low’ & ‘high’ refer to low (<1,250m) and high (>1,250m) elevation sample data.

Plant (2013) proposed that most species of *Hybos* occurring in Thailand could be systematically assigned to 8 informal species-groups based largely on genital morphology. While species-level endemism is apparent in all 8 groups, only the *Hybos tetricus*-group appears to be entirely confined to Thailand (at low elevation in the southern Tenasserim Hills and Cardamom Mountains) and there is thus little congruence between systematic position and contemporary distributions adopted by the species-groups in Thailand. Although some species could not be assigned to a species-group, and might themselves constitute taxa with the same ranking as the species-groups, it is clear that for most taxa, the historical factors promoting diversification into species-groups likely acted independently of, and are older than those promoting more recent within-group speciation. Further evidence of the age and ubiquity of species-groups might be inferred from the observation that most species-groups are represented in communities corresponding with area clades recovered in ‘basal’ polytomy by PAE and EZPAE (Figs. 2–5) although the basal polytomy might be considered non-informative, simply reflecting a failure to resolve the area relationships. Many Empidoidea and most Hybotinae (including especially *Hybos*) occurring in Southeast Asia appear to be ‘old’ Oriental elements (Chvála, 1983; Grootaert, 2009; Plant et al. 2011; Plant, 2013) and the taxa occurring in the geographic areas of the ‘basal’ polytomy are considered here to reflect this. Taxa represented in the terminal area clades of the northern and western mountains (clade-2, Fig. 5) and the south-eastern ranges (clade-3, Fig. 5) appear to have been derived from the old Oriental elements of the ‘basal’ polytomy, and it is these same mountain ranges (especially the Daen

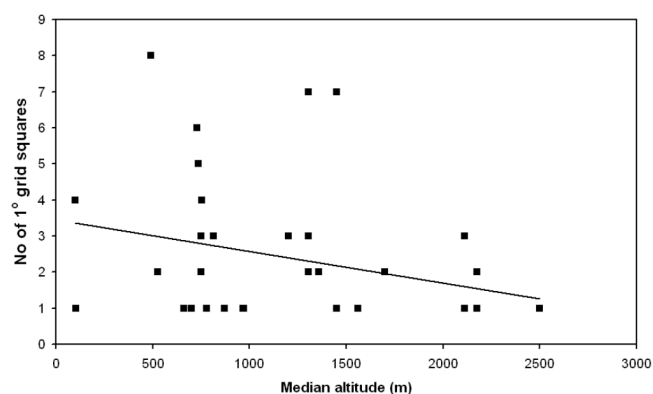


Fig. 6. Relationship between elevation and geographical range of *Hybos* spp. in Thailand. The number of 1° grids in which a species was recorded is plotted against the median elevation of all records. Line fitted by linear regression in PAST ($r^2=0.1026$).

Lao and Thanon Thongchai) which have highest levels of species richness (Fig. 1B) and local endemism (Fig. 1C). Interestingly, there is a weak negative correlation ($r^2=0.1026$) between the number of 1° grids in which a species is present and the median altitude at which it occurs (Fig. 6); species occurring at lower elevations tend to be more widespread, and furthermore, they contribute mostly to the ‘basal’ polytomy reported in PAE and EZPAE (for a detailed account of the altitude range of each species see Plant, 2013). Overall, the evidence tentatively suggests that hotspots of *Hybos* diversity and endemism in Thailand have arisen from relatively recent radiation on certain mountain chains from a ‘background’ of older taxa, with Oriental affinities and more ubiquitous distribution. *Hybos* is probably still speciating actively in Thailand as for example, *H. phahompokensis* Plant from the Daen Lao and *H. inthanonensis* Plant from the nearby Thanon Thongchai ranges are extremely similar species separated from each other primarily by small differences of the male terminalia. Similarly, small differences in the male terminalia of *H. serratus* Yang & 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 montane populations (Plant, 2013).

What factors could have driven radiation of *Hybos* in Thailand’s mountains? The orogenesis of the western and northern mountains was coincident with the development of a seasonally more arid monsoon climate and was punctuated by periods of climatic drying associated with Pleistocene glacial episodes. The northern and western axial mountains of Thailand were uplifted following the collision of India with Eurasia ~50MYA (Royden et al., 2008). The collision also resulted in the elevation of the Tibetan Plateau and initiated a seasonal monsoon climate perhaps as early as 15–20MYA (Harris, 2006). During the Miocene (10–23 MYA) Southeast Asia’s climate was probably warmer with less seasonally dependant precipitation and tropical rainforests may have extended as far north as Yunnan in southern China (Heaney, 1991; Zhu, 2008). Throughout the Pleistocene, progressive climatic cooling and modified rainfall regimes caused a southwards retreat of tropical forests

(Heaney, 1991; Voris, 2000; Penny, 2001). During glacial maxima, montane vegetation and pine-grassland savannah were more prominent (Heaney, 1991; Brandon-Jones, 1998) and evidence from mammals (Brandon-Jones, 1998), plants (Werner, 1997; Canon & Manos, 2003) and palynological deposits (Penny, 2001) indicate substantial migrations of Southeast Asian biota in response to climatic drying and cooling during this period. Amongst Diptera, Pleistocene environmental changes have strongly influenced historical patterns of population fragmentation and survival in refugia followed by migration and recolonisation in, for example, Culicidae (O'Loughlin et al., 2008; Morgan et al., 2011) and Simuliidae (Pramual et al., 2005, 2011; Pramual & Wongpakam, 2013).

Plant et al. (2012) hypothesised that in the nascent mountain ranges, seasonality was relaxed with more aseasonal moist conditions prevailing at higher elevations. The biota of increasingly dry lowland forests was able to partition into and speciate in the newly emerged aseasonal moist montane forests which thus functioned as climatically buffered refugia where it could survive and subsequently radiate. In this study, when OGU's were segregated on altitude and 'characters' made additive, EZPAE resolved an area clade comprising the Tenasserim Hills, Daen Lao and Thanon Thongchai ranges in which low elevation OGU's for all three mountain ranges occupied 'basal' positions in respect to high elevation OGU's (clade-2, Fig 5). These results suggest that in these northern and western mountains, the *Hybos* fauna of high elevations may have been derived from that at lower elevation within the same group of mountains and are entirely consistent with the Climate History Model of Plant et al. (2012).

That contemporary endemism and species richness is greatest in montane areas suggests that *Hybos* has not easily recolonised lowlands and that lowlands have functioned as barriers to population divergence. However, it should be considered that there are also several examples of widespread lowland species (e.g., *H. particularis*, Yang, Yang & Hu, *H. xishuangbannaensis* Yang & Yang and perhaps *H. thaosaeo* Plant) which must historically have been able to disperse effectively at low elevations. While endemic *Hybos* communities at higher altitudes in the northern and western mountains may have been derived relatively recently from ancestral lowland communities, they occur alongside species such as *H. apicihatatus* Yang & Yang, *H. zhejiangensis* Yang & Yang and *H. longus* Yang & Yang which are widespread in China, but which in Thailand are found only on the highest mountains of the north where they may be at the southernmost extremities of their ranges (Plant, 2013). Such species may be the products of an earlier radiation and dispersal event than that responsible for modern endemism discussed above. Altitudinal partitioning between seasonal lowlands and aseasonal highlands is but one of several mechanisms that may have contributed to the composition of modern *Hybos* communities in Thailand and while it appears to have been important in originating the diversity and endemism associated with an apparently ongoing radiation in the north and west, faunal composition has also been influenced by the dispersal of lowland-adapted 'old' Oriental elements

and very probably by historical radiation and dispersal from geographically remote refugia. Understanding the relative importance and timing of these different mechanisms with require detailed phylogenetic and phylogeographic analysis.

ACKNOWLEDGEMENTS

I would like to thank the many people who collected the material that made possible the taxonomic revision without which this work would not have been possible. For access to Thailand Insect Group for Entomological Research (TIGER) material I am indebted to Brian Brown and Michael Sharkey. Wichai Srisuka made available material from the High Land Project and other sampling efforts undertaken by Queen Sirikit Botanic Garden Entomology Section and special thanks are due to Raewat Saokhod and Chayanit Surin for their sorting of specimens and accurate recording of data. Chaweewan Hutacharern is thanked for her indefatigable support throughout. The Thailand National Parks Department allowed access to protected areas and the TIGER Project was supported by the USA NSF (grant no. DEB-0542846).

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