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Elevational Gradients of Diversity and Species Composition of Hemerodromiinae (Diptera: Empididae) at Doi Inthanon, Thailand: Has Historical Partitioning between Seasonally Dry Lowland and Aseasonal Moist Mountain Forests Contributed to the Biodiversity of Southeast Asia?

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ABSTRACT.– Community structure, species richness and diversity of Hemerodromiinae (Diptera: Empididae) were investigated along an altitudinal gradient between 700 m and 2,500 m above mean sea level on the Doi Inthanon mountain in northern Thailand (18º 35’ N, 98º 29’ E). The diversity and richness were maximal at the upper-mid to sub-summit elevations corresponding to speciose communities associated with continually moist montane evergreen forests. A relatively depauperate species assemblage was associated with seasonally water-stressed biotopes at lower elevations. Relaxation of seasonal aridity at higher elevations was considered an important determinant of species richness and abundance for Hemerodromiinae, especially Chelipodini which require moist soils for development. Elevational patterns of strictly aquatic Hemerodromiini were reasoned to arise from geometrical constraints limiting the number of suitable streams at altitudinal extremes.- there are more water courses at intermediate altitudes where abundance and diversity are greatest. Historical factors underlying current diversity and abundance patterns are discussed and hypothesised to involve three elements. (1) Historically concurrent orogenesis of mountain ranges, development of a seasonally arid monsoon climate in Southeast Asia and dry periods associated with glacial maxima forced altitudinal migrations into and subsequent radiation in aseasonal moist forests that developed on nascent mountains. (2) Immigration from the northwest and south along ‘corridors’ of montane moist forest, and (3) dispersal of lowland forms inhabiting seasonally dry biotopes in response to climatic drying.

KEY WORDS: Diptera, Empididae, Hemerodromiinae, altitude, phylogeography

INTRODUCTION

The Empididae (Diptera) subfamily Hemerodromiinae contains 18 extant genera of small predatory flies with inflated raptorial forelegs. Two phylogenetically distinct tribes are recognised (Plant, 2011); Chelipodini in which immature stages are associated with moist soils in humid biotopes, and Hemerodromiini which have strictly aquatic larvae and pupae associated with lotic and lentic freshwater habitats. In Thailand, Chelipodini are represented by *Chelipoda* Macquart, *Achelipoda* Yang, Zhang and Zhang and *Anaclastoctedon* Plant (Plant, 2009a, b, 2010), whilst Hemerodromiini are represented by *Chelifera* Macquart and *Hemerodromia* Meigen (Horvat, 2002; pers. obs). Although Hemerodromiinae are widespread and often abundant on Thailand’s mountains, little is known of their ecology except for a study of seasonal and altitudinal abundance of *Chelipoda* (Plant, 2009a). The present study investigated the influence of elevation on community structure, diversity and species richness between 700 m and 2,500 m (all altitudes are given as height in meters above the mean sea level) on Thailand's highest mountain, Doi Inthanon (2,565 m). The phylogeographic history of highly water-dependant Hemerodromiinae is discussed with reference to the historical development of a seasonally dry monsoon climate, aridity associated with past glacial maxima and mountain orogenesis in Southeast Asia.

MATERIALS AND METHODS

Materials used in this study was collected during 2006 and 2007 as part of a three year invertebrate sampling project (TIGER– Thailand Insect Group for Entomological Research) using only material collected on the mountain Doi Inthanon in Chiang Mai Province, northern Thailand. Doi Inthanon (18º 35' N, 98º 29' E) is a metamorphic core complex bounded by low angle faults which has been uplifted (MacDonald et al., 1993; Dunning et al., 1995; M. Searle, pers. com.) and its summit at 2,565 m is now considerably higher than the surrounding mountains. Its large altitudinal variation supports a variety of altitudinal succession zones ranging from dry dipterocarp forest on the lower slopes through to extensive moist hill evergreen forest and peat bog about the summit.

Malaise traps were operated continuously for one year at 700 m, 1,200 m, 1,700 m, 2,200 m and 2,500 m on the slopes of the mountain. Traps were emptied weekly and described Hemerodromiinae identified using Plant (2009, 2009a, 2010). Undescribed Hemerodromiinae were determined at generic level and assigned to morphospecies using morphological characters consistant with the current understanding of Hemerodromiinae taxonomy. The abundance and number of species recorded at each altitude station were recorded. All statistical analyses employed PAST (Hammer et al., 2001) except regression analysis which was performed with Microsoft Excel. Diversity was calculated as the Shannon index *H* and Fisher's alpha. The extent to which individual taxa dominated communities was measured as Dominance *D* (1- Simpson index) and Berger-Parker dominance. The evenness with which individuals are distributed among the taxa present was determined as Equitability *J* (Harper, 1999; Hammer et al., 2001; Hammer and Harper, 2006). Relationships between species assemblages were investigated by (1) ordination using non-metric multidimensional scaling by employing Bray-Curtis similarity indices to compute a minimal spanning tree from the similarity matrix of included taxa, and (2) Cluster analysis using unweighted pair-group average and Bray-Curtis similarity indices.

Abbreviations.– **Ach_kha**, *Achelipoda khakhema* Plant, 2009; **Ana_ant**, *Anaclasto ctedon antarai* Plant, 2010; **Ana_lek**, *Anaclastoctedon lek* Plant, 2010; **Ana_spT**, *Anaclastoctedon* sp. T (*sensu* Plant, 2010); **Che_sp1**, *Chelifera* sp. 1; **Che_sp2**, *Chelifera* sp. 2; C**_chai**, *Chelipoda chaiamnata* Plant, 2009; **C_flav**, *Chelipoda flavida* Brunetti, 1913; **C_hube**, *Chelipoda hubeiensis* Yang and Yang, 1990; **C_inth**, *Chelipoda inthawichayanona* Plant, 2009; **C_kame**, *Chelipoda kameawuta* Plant, 2009; **C_lais**, *Chelipoda laisoma* Plant, 2009; **C_macr**, *Chelipoda macrosceles* Plant, 2009; **C_mang**, *Chelipoda manggawna* Plant, 2009; **C_meen**, *Chelipoda*

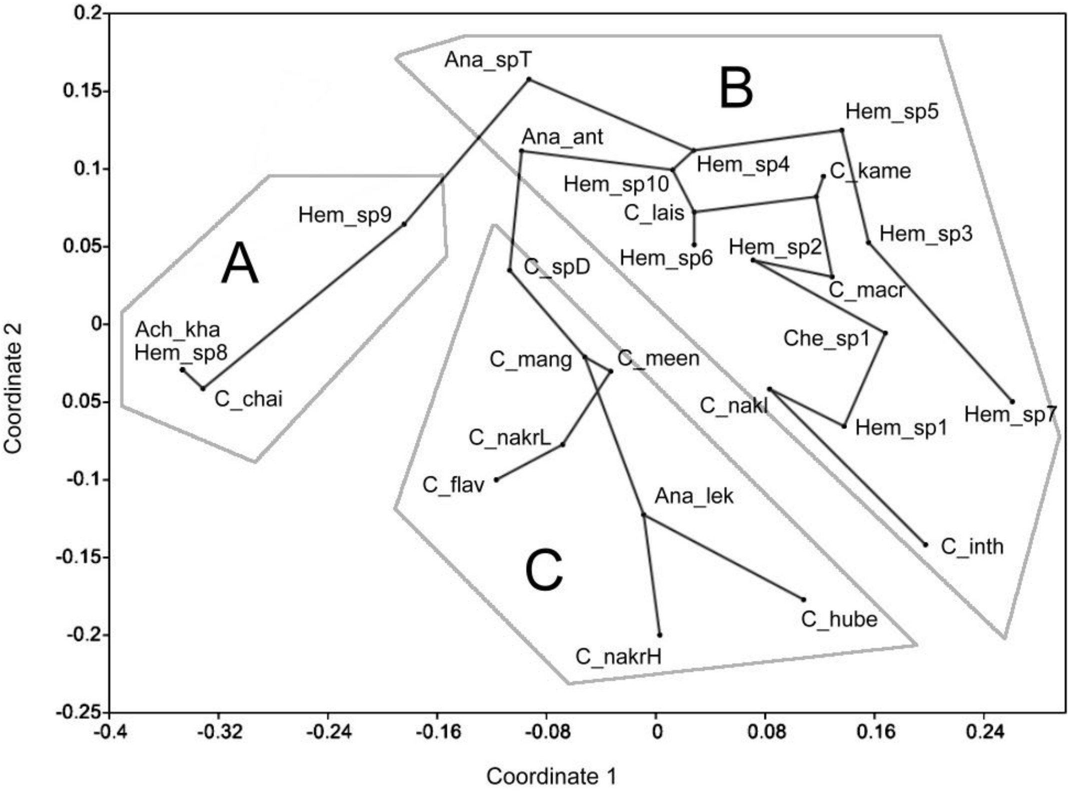

FIGURE 1. Minimal spanning tree of similarity matrix calculated by non-metric multidimensional scaling using Bray-Curtis similarity. Species assemblages A, B and C are indicated.

meenamluang Plant, 2009; **C_nakl**, *Chelipoda nakladam* Plant, 2009; **C_nakrH**, *Chelipoda nakropa* Plant, 2009 (high elevation morph); **C_nakrL**, *Cheli-poda nakropa* Plant, 2009 (mid elevation morph); **C_spD**, *Chelipoda* sp. D (*sensu* Plant, 2009); **Hem_sp1**, *Hemerodromia* sp. 1; **Hem_sp2**, *Hemerodromia* sp. 2; **Hem_sp3**, *Hemerodromia* sp. 3; **Hem_sp4**, *Hemerodromia* sp. 4; **Hem_sp5**, *Hemerodromia* sp. 5; **Hem_sp6**, *Hemerodromia* sp. 6; **Hem_sp7**, *Hemerodromia* sp. 7; **Hem_sp8**, *Hemerodromia* sp. 8; **Hem_sp9**, *Hemerodromia* sp. 9; **Hem_sp10**, *Hemerodromia* sp. 10.

RESULTS AND DISCUSSION

A total of 961 individuals belonging to 29 species / morphospecies and 5 genera were collected in Malaise traps along the elevational transect. The following genera were represented (with number of species / morphospecies and number of individuals in parenthesis):- *Chelipoda* (13, 799), *Achelipoda* (1, 1), *Anaclastoctedon* (3, 99), *Hemerodromia* (10, 53) and *Chelifera* (2, 9). *Chelipoda nakropa* Plant, 2009a exists in two morphologically distinct but altitudinally segregated morphs (Plant, 2009) and for the purposes of this analysis both morphs were treated as separate taxa. Most individuals of *Chelipoda, Achelipoda* and *Anaclastoctedon* were determined as

TABLE 1. Diversity parameters for Hemerodromiinae at different altitudes on Doi Inthanon.

Altitude (m)	700	1200	1700	2200	2500
No of taxa	2	7	15	19	14
No of individuals	3	41	283	445	189
Shannon index (H)	0.636	0.894	1.739	1.355	1.414
Fisher alpha	2.622	2.427	3.378	4.031	3.492
Dominance (D)	0.557	0.619	0.239	0.404	0.387
Berger-Parker dominance	0.667	0.78	0.329	0.596	0.593
Equitability (J)	0.918	0.459	0.642	0.46	0.535

previously described species. All the individuals of *Chelifera* and *Hemerodromia* probably represent undescribed species and are treated as un-named morphospecies.

Community Structure.– A minimal spanning tree of the similarity matrix calculated by non-metric multidimensional scaling using Bray-Curtis similarity resolved a three-branched hierarchy of assemblages of taxa (Fig. 1). Group A comprised species that mostly occur at 1,200 m, corresponding with vegetational transitions between lower and dry mixed deciduous or pine forest into rather less seasonally water-stressed evergreen forest. Taxa in Group C generally had wide altitudinal ranges between 1,700 m and 2,500 m (only occasionally lower) and may represent a cosmopolitan group persisting in a wide range of Hill Evergreen forest types. Group B was the largest assemblage and was almost entirely restricted to the upper Moist Hill Evergreen forest between 2,200 m and 2,500 m.

Cluster analysis (Fig. 2) retrieved with reasonable bootstrap support, a cluster of species identical with Group A obtained by ordination. Groups B and C were also resolved, albeit with weak support.

Diversity.- The total number of taxa and individuals of Hemerodromiinae increased with altitude, declining above a maxima at 2,200 m (Table 1). The diversity parameters, Fisher's alpha and Shannon index *H*, were also positively correlated with altitude but the Shannon index *H* declined above a maximum at about 1,700 m (Table 1 and Fig. 3). Linear regression revealed a rather weak correlation of Fisher's alpha (r^2 = 0.700) and Shannon index (r^2 = 0.568) with altitude. When data were fitted to a binomial, a similarly weak correlation with altitude was found for Fisher's alpha (r^2 = 0.703) but Shannon index was more strongly correlated (r^2 = 0.781) (Fig. 3) The higher values of these diversity measures may reflect communities rich in taxa but relatively impoverished with numbers of individuals. In contrast, the Berger-Parker values and Dominance *D* provided an almost opposite relationship as they reached maxima at 1,200 m and then decreased to minima at 1,700 m above which they increased again (Table 1). The higher values of the dominance parameters suggest that large numbers of individuals of relatively few taxa tend to dominate a community. The Equitability value *J* was highest at the lowest elevation but thereafter showed no clear trend with increasing elevation (Table 1).

Species richness and abundance of individual genera is shown in Table 2. Species richness for *Chelipoda* increased with altitude to an horizontal asymptote at and beyond 2,200 m, but for *Hemerodromia*, although it also increased with altitude up to a maximum at 2,200 m,

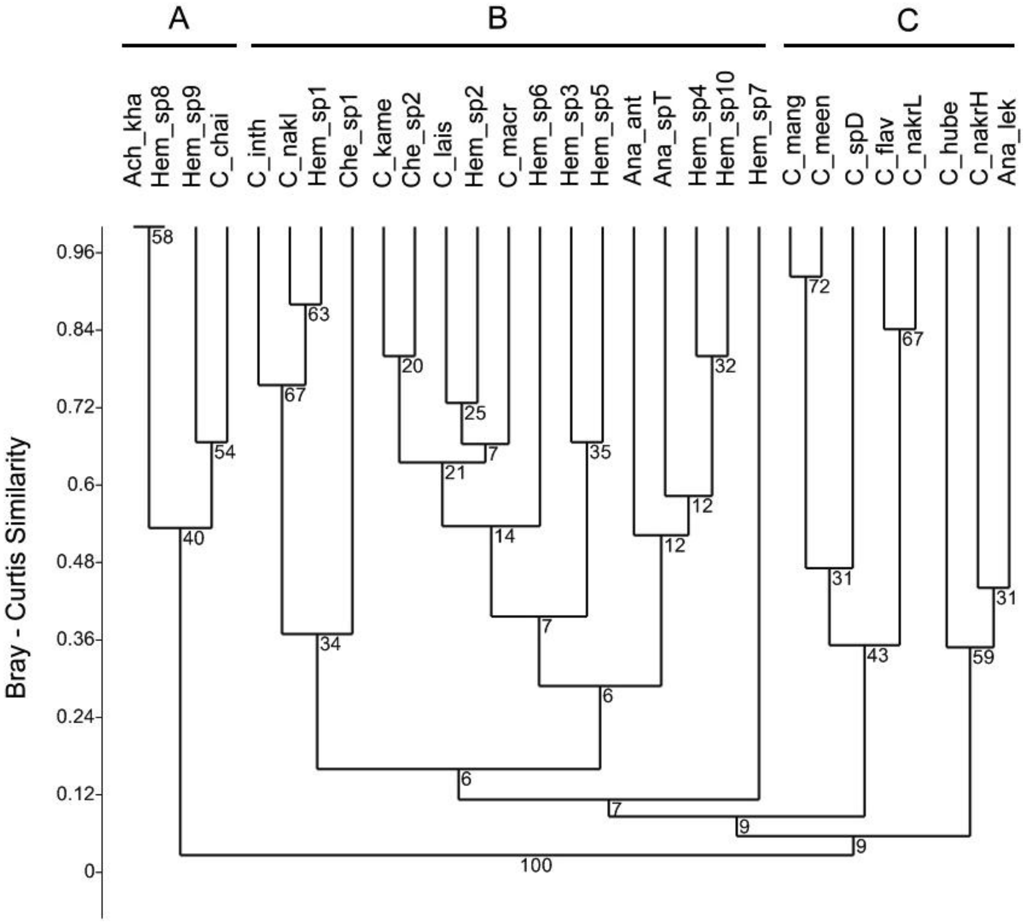

FIGURE 2. Cluster analysis using unweighted pair-group average and Bray-Curtis distance indices. Bootstrapping was performed with 1000 resamples; the percentage of replicates where each node is still supported is shown. Species components in clusters A, B and C correspond with the species assemblages A, B and C previously resolved by non-metric multidimensional scaling (see Fig. 1).

richness then declined sharply at 2,500 m. *Chelifera* was confined to between 2,200 - 2,500 m and *Anaclastoctedon* between 1,700 - 2,200 m. *Achelipoda* was represented by a single individual at 1,200 m.

The relative merits and demerits of various indices used to measure changes in diversity along environmental gradients have been widely discussed. There is however, agreement that their use has successfully established a general paradigm that diversity and richness decreases with increasing altitude and latitude (e.g. Gathorne-Hardy et al., 2001; Hillebrand, 2004; Palin et al., 2011). Another frequently reported relationship between species richness and altitude is the occurrence of a peak at mid elevations (Rahbek, 1995; Lomilino et al. 2001; Colwell et al., 2004). Although geographical gradients in species richness are often reasoned to reflect underlying abiotic, ecological or evolutionary factors, random placement of geographic ranges within a bounded map

TABLE 2. Generic composition of Hemerodromiinae at different altitudes on Doi Inthanon. For each genus the number of species or morphospecies is given followed by the total number of individuals in brackets.

Altitude (m)	**700**	**1200**	**1700**	**2200**	**2500**
Chelipodini					
Chelipoda	2 (3)	4 (36)	7 (257)	9 (341)	9 (162)
Achelipoda	- (-)	1 (1)	- (-)	- (-)	- (-)
Anaclastoctedon	- (-)	- (-)	3 (19)	1 (80)	- (-)
Hemerodromiini					
Hemerodromia	- (-)	2 (4)	5 (7)	7 (20)	4 (22)
Chelifera	- (-)	- (-)	- (-)	2 (4)	1 (5)

can produce a peak of species richness near the centre.- the Mid Domain Effect (MDE). The effect is stochastic, arising through simple geometric constraints and has been supposed to provide a null hypothesis, obviating the need for otherwise abiotic or biotic causation (Colwell and Hurtt, 1994; Jetz and Rahbek, 2001; Colwell et al., 2004).

The peaks of Hemerodromiinae diversity, species richness and abundance reported here from intermediate and sub-summit altitudes on Doi Inthanon might be due to a MDE, but even if this is so, it seems likely that climatic and ecological influences are superimposed upon it. Immature stages of *Chelifera*, *Hemerodromia* and other genera included in the tribe Hemerodromiini are found in water bodies varying from seepages, streams, large rivers and lakes. They exhibit specific adaptations to fresh water (Brammer et al., 2009) where their larvae prey on small invertebrates (Vaillant, 1981; Hamada, 1993; Harkrider, 2011). Adults are often recovered in emergence traps over water (Wagner et al., 2004) and are seldom found far from water bodies. So far as it is known (Plant, 2007, 2011) larvae of Chelipodini are probably predatory on soil invertebrates but, unlike Hemerodromiinae, adult Chelipodini are found frequently in damp forest biotopes far removed from water bodies.

It is probable that the presence and abundance of Chelipodini is largely governed by a requirement for moist soils determined by edaphic, climatic and vegetation structural factors. The lower slopes of Doi Inthanon, below about 800 m, are covered with deciduous forest types which experience pronounced aridity during the dry season. Seasonally drought-tolerant semi-evergreen, dry evergreen and pine forest continues to about 1,200 m above which less drought-tolerant evergreen forests predominate. We suspect that seasonally arid soils are a major factor demarking the lower elevational limit of Chelipodini and account for the low species richness below 1,200 m reported here. Indirect support for this hypothesis was provided by an analysis of seasonal phenology of *Chelipoda* at different altitudes on Doi Inthanon (Plant, 2009a) which found that above 1,700 m, species richness was slightly greater during the dry season compared with the wet season but the pattern was reversed at lower altitudes. It was hypothesised that outside the wet season, the seasonal drought experienced on the lower slopes of the mountain results in conditions which are less suitable for *Chelipoda* but that seasonality is relaxed on the upper slopes which maintain a suitable moist environment even in the dry season.

Although cluster analysis and ordination did not provide any evidence for generic-level assemblages of taxa, despite their

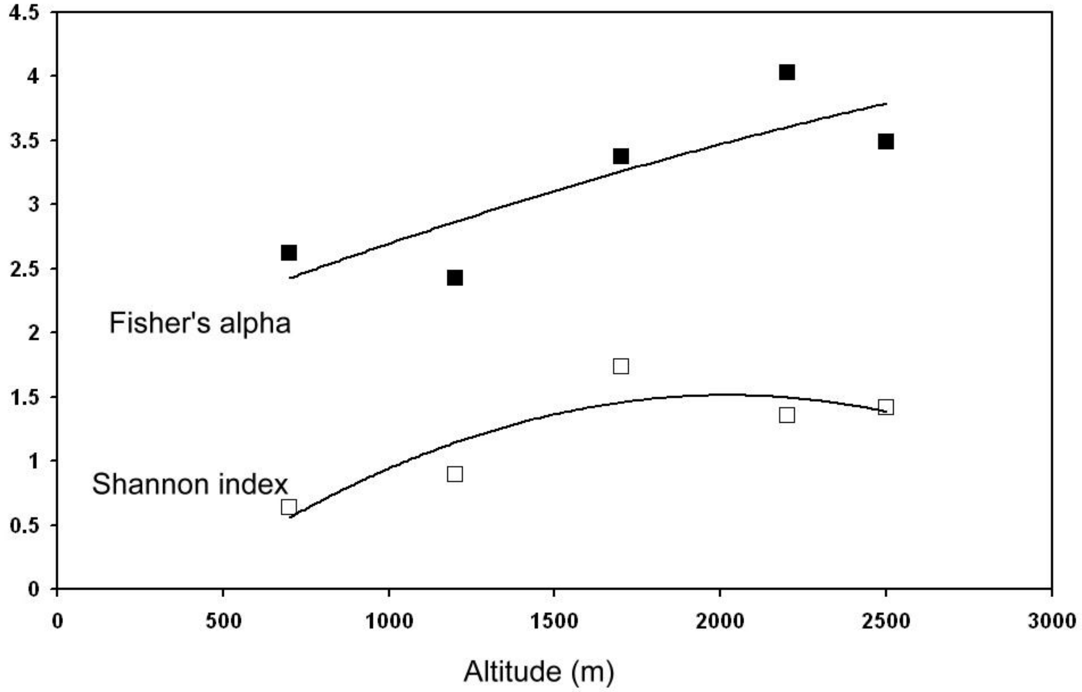

FIGURE 3. Relationship of Fisher's alpha and Shannon index to the altitude for Hemerodromiinae sampled at various elevations on Doi Inthanon. Data are fitted to a binomial; closed symbols, Fisher's alpha (r2 = 0.701); open symbols, Shannon index (r2 = 0.781).

differences in life history, the requirement of Hemerodromiini for free water might suggest that because streams flow down the lower slopes of the mountain (trap sites at 700 m and 1,200 m were close to water bodies), species richness could be less negatively influenced by surrounding seasonally arid conditions. However, no Hemerodromiini were found below 1,200 m and species richness increased with altitude with the genus *Hemerodromia* peaking in the sub-summit zone at 2,200 m. The summit zone around 2,500 m has few streams (trap sites at 2,500 m were in forest adjacent to a rain-fed peat bog). Many streams issue slightly lower down and flow through mid-elevations to coalesce into larger rivers on the lower slopes. The peak in richness at mid to sub-summit elevations could thus be a consequence of simple geometrical constraints limiting the number of suitable streams within a given geographical area at altitudinal extremes.- there are more water courses at mid to sub-summit elevations.

The richness of *Chelipoda* in Hill Evergreen and Moist Hill Evergreen forests on Doi Inthanon has been documented previously (Plant, 2009a) and the data presented here demonstrate a similar enrichment of most, if not all Hemerodromiinae genera in the upper forests. Extensive collecting of Hemerodromiinae throughout Thailand (mostly by the TIGER Project) has yielded large numbers of Hemerodromiinae. This material has yet to be thoroughly studied but it is immediately apparent that many undescribed taxa are represented and that the majority were trapped in characteristically moist montane

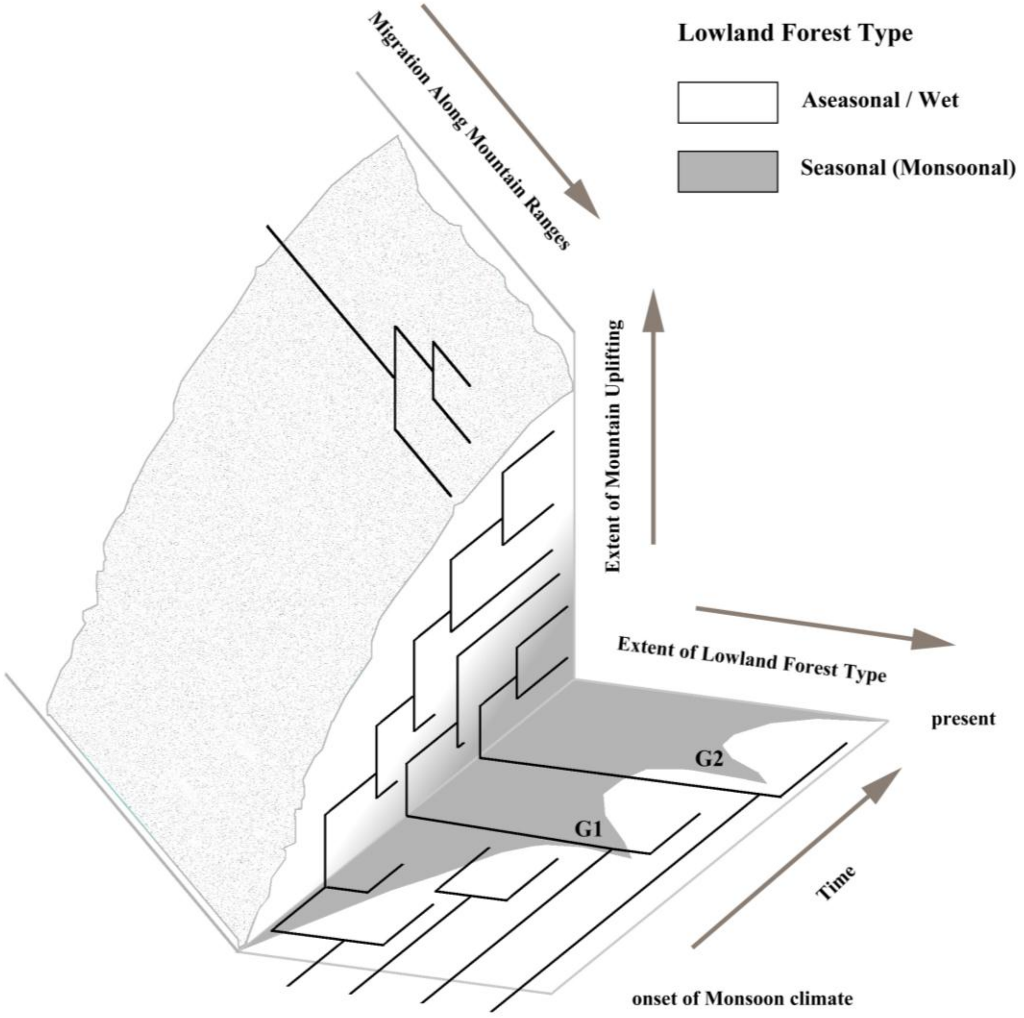

FIGURE 4. Schematic illustrating radiation of Hemerodromiinae in Thailand's mountains. The horizontal plane of the figure shows how the proportion of seasonally dry (monsoonal) forest has increased historically with 'spikes' of aridity during glacial maxima (G1 and G2). Concurrent uplifting of new mountain ranges (vertical plane) resulted in moist aseasonal forest into which taxa that failed to adapt to increasing aridity could migrate altitudinally and radiate. Connectivity with distant mountain ranges along mountain ridges provided 'corridors' of wet forest through which migration occurred from outside the region.

evergreen forests. Very few were trapped in seasonally arid lowland deciduous forest excepting a small number of Hemerodromiini which were probably associated with lowland watercourses. The relaxation of seasonal drought-stress at higher elevations is probably an important determinant of species richness and abundance for all Hemerodromiinae.

GENERAL DISCUSSION

The mountains of northern and western Thailand are situated within the Indo-Burma biodiversity hotspot recognized by Myers et al. (2000) as globally significant. Thailand's N-S axial mountains were uplifted at varying rates during the Cenozoic following the collision of India with Eurasia ~50 MYA (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 15–20 MYA (Harris, 2006) with profound biotic consequences. During the Miocene (10–23 MYA) Southeast Asia's climate was probably warmer than at present with less seasonally dependant rainfall and tropical rainforests may have extended as far north as Yunnan, southern China (Heaney, 1991; Zhu, 2008). During the Pleistocene, the climate experienced progressive general cooling and modified rainfall regimes (Heaney, 1991; Voris, 2000; Penny, 2001) and tropical forests responded by retreating southwards. During glacial maxima montane vegetation and pine-grassland savannah were more prominent (Heaney, 1991; Brandon-Jones, 1998) and evidence from plants (Werner, 1997; Canon and Manos, 2003), palynological deposits (Penny, 2005), mammals (Brandon-Jones, 1998) and aquatic Diptera (Pramual et al., 2005, 2011; O'Loughlin et al., 2008; Morgan et al., 2010 for example, indicate substantial migrations of southeast Asian biota in response to climatic drying and cooling during this period.

Modern Southeast Asian tropical rainforests have a rich but largely undescribed Hemerodromiinae fauna (Plant, 2011; unpublished data). Aquatic Hemerodromiini and ombrophilous Chelipodini inhabiting Southeast Asia's Miocene rainforests may have been especially sensitive to increased seasonal drought conditions imposed by the developing monsoon cycle and to dry periods correlated with Pleistocene glacial maxima. The obligate water-dependency of Hemerodromiinae would have mitigated against adaptation to climatic drying and driven altitudinal migration into seasonally buffered montane refugia (Fig. 4). A range of altitudinal succession zones in close approximation on the mountains' slopes would have facilitated dynamic vertical dispersal into mountain refugia as environmental and vegetation patterns changed, with populations subsequently becoming isolated and radiating on the mountains as orogenesis and climate change continued. Support for the past existence of montane refugia of aquatic Diptera in Thailand has been provided, for example, by population history studies based on mtDNA sequences of two species of *Simulium* (Diptera, Simuliidae), the ancestral haplotypes of which appear to have survived glacial maxima in moist montane refugia (Pramual et al., 2005, 2011).

The upper slopes of Thailand's northern mountains share at least some affinities with the Palaearctic Realm (Hara et al., 2002; Plant, 2008). It is possible that some Palaearctic elements may have penetrated the Oriental along 'corridors' of suitable cool moist forest on easternmost mountain folds of the Himalaya during their orogenesis in the mid to late Cenozoic. Here they would have contributed to diversity on the mountains but seasonal dryness may have prevented colonization of the lowlands.

Resolution of Palaearctic and Oriental elements of Thailand's Hemerodromiinae awaits detailed phylogeographic evaluation but the results of a tentative phylogeny and biogeographical analysis of the subfamily (Plant, 2011) provide some insight. The 77 described species of *Chelifera* are more or less confined to the Northern Hemisphere with species richness highest in the mountains of Europe and in the western Himalaya and rather less so in the eastern and western mountains of North America. Only six species are recorded from China and just two from Thailand and it does not appear to have spread into Indonesia. A fossil has been found in Eocene/Oligocene Baltic amber and *Chelifera* appears to have originated in Eurasia and may be a relatively recent colonist in the Oriental. In Thailand, *Chelifera* is apparently confined to the upper slopes of higher mountains, as in this study all examples of *Chelifera* were trapped at or above 2,200 m, while Horvat (2002) described *C. malickyi* from 2,100 m on Doi Inthanon and *C. thaica* from the upper slopes of Doi Suthep-Pui (1,685 m). The preference of *Chelifera* for high mountains and its likely centre of radiation in Palaearctic mountains suggests that it is a candidate for dispersal into the Oriental along montane corridors.

Hemerodromia is a speciose genus, probably of relatively recent origin in Eurasia where current diversity is greatest (at least for described species) and a late Eocene fossil is known from Ukrainian amber. From its northern loci of dispersal it has reached southern Africa, all but the most southerly parts of South America and into the SW Pacific and Australia where dispersal seems to have been constrained by the late Miocene drying of the continent. It is apparently species-rich in Southeast Asian rainforests (although the fauna is largely undescribed) and is likely to have survived climatic drying in Thailand by dispersal into mountain refugia.

The systematics of *Chelipoda* and closely related genera are poorly resolved and although basal groups of the Chelipodini may have had southern origins, *Chelipoda* is now widespread and the clade containing all the Thailand species is represented throughout Eurasia, the Americas and in Australia although it does not seem to have reached Africa, Oceania or New Zealand. It is most speciose in damp, humid forest biotopes and apparent centers of diversity in Southeast Asia and southern Chile probably reflect little more than recent taxonomic revisionary work in these areas and the fact that there is an abundance of suitable habitat. The related genus *Achelipoda* is endemic to eastern Asia occurring from Taiwan to Indonesia with three described species in Thailand. In Thailand *Achelipoda* species have been recorded between 660 m and 1,200 m, mostly in the east of the country and mostly from dryer forest types including pine-grassland savannah. It is possible that its dispersal history may have been facilitated by episodes of climatic drying.

Anaclastoctedon is a small genus with only five described species, including two in Thailand. It probably had a southern temperate origin, dispersing from Australia into Asia as Australia drifted northwards during the Tertiary, exploiting increasing connectivity between the high mountains of eastern Australia and Asia. A northwards migration along Southeast Asian mountains has probably occurred. In Asia it has penetrated as far as Nepal and there are further undescribed species in the mountains of Thailand and Vietnam.

It seems likely that multiple dispersal patterns and partitioning between seasonally arid lowlands and moist aseasonal mountains during periods of climate change may have been an important determinant of diversity and abundance of Hemerodromiinae in Thailand’s mountains. Altitudinal migration into newly arisen ‘niche-space’ occasioned by the historical coincidence of mountain orogenesis and climatic drying may have provided a general mechanism of biotic enrichment of Southeast Asia's mountains with continued uplifting leading to increased isolation and radiation of marooned taxa. The exceptional diversity of the regions wet montane forests can be viewed to have arisen from historical altitudinal displacement of lowland rainforest biota augmented by immigration from outside the region along montane 'corridors' of moist forest.

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