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Endemism, Similarity and Difference in Montane Evergreen Forest Biodiversity Hotspots: Comparing Communities of Empidoidea (Insecta: Diptera) in the Summit Zones of Doi Inthanon and Doi Phahompok, Thailand

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ABSTRACT.– Composition and structure of communities of the Diptera superfamily Empidoidea (30,481 individuals of 511 species in 55 genera in the families Empididae, Dolichopodidae, Hybotidae and Brachystomatidae) were compared in Upper Montane Forests on Doi Inthanon and Doi Phahompok in northern Thailand. Based on taxon similarity (α-, β-diversity), structural diversity (the species abundance distribution and importance of dominant species), cluster analysis of community composition and the relative importance of inferred Oriental and Palaearctic influences, it was concluded that communities in Upper Montane Forest at 2,036 – 2,105 m near the summit of Doi Phahompok were most similar to those at 1,639 – 2,210 m on Doi Inthanon. Approximately 33% of species recorded at 2,036 – 2,105 m on Doi Phahompok were endemic to the mountain. Upper Montane Forest is a rare, dispersed and isolated habitat in southeastern Asia with scattered patches likely to experience comparable levels of β-diversity and endemism as found here. The conservation importance of Upper Montane Forest on Doi Phahompok and on other mountains in northern Thailand is stressed. The upper slopes of Doi Inthanon (>2,200 m) are reaffirmed as a unique haven of endemic species and distinctive Empidoidea communities in a habitat judged to be of utmost conservation interest.

KEY WORDS: conservation, Brachystomatidae, Dolichopodidae, Empididae, Hybotidae

INTRODUCTION

Diptera (true flies) are one of the megadiverse and abundant insect orders that contribute greatly to the biodiversity of tropical forests and are major components of the exceptionally rich biodiversity of insects in the montane evergreen forest of northern Thailand (Plant et al., 2018). The Diptera superfamily Empidoidea (represented in Thailand by the families Empididae, Dolichopodidae, Hybotidae and Brachystomatidae) is a large and important taxon comprising approximately 10% of global fly diversity. A recent study of Empidoidea on the mountain Doi Inthanon in northern Thailand (Plant et al., 2019) identified three major habitat and elevation delimited community-types (designated Moist Hill Evergreen, '*MHE*' [>2,000 m]; Mid Elevation Evergreen '*EM*' [1,000 – 2,000 m] and Dry Lowland '*DL*' [<1,000 m]; the names specifically refer to dipteran communities, even though they reference characteristics of the forests in which the communities were found). The occurrence of *MHE*, *EM* and *DL* fly communities corresponded well with the occurrence of formal forest types resolved by Santisuk (1988) and designated as Upper Montane Forest (at >1,800 m), Lower Montane Forest (at 1,000 – 1,800 m) and Lowland Deciduous Forest (at <1,000 m) respectively. Because the elevational succession of Upper Montane Forest - Lower Montane Forest - Lowland Deciduous Forests with which *MHE*, *ME* and *DL* Diptera communities are associated is widespread in northern Thailand, it is likely that the description of diversity characteristics of fly communities found on Doi Inthanon is scalable over a much wider geographic area (Plant et al., 2019), albeit with community turnover and local endemism influences superimposed.

Montane evergreen forests occur widely in northern Thailand where they are important but threatened centres of biodiversity (Pattanavibool and Dearden, 2002) and this is especially true of Upper Montane Forest which is a rare habitat, mostly restricted to a few mountains in the Thanon Thongchai, Den Lao, Khun Tan and Luang Prabang ranges that rise above 1,800 m. The most extensive tracts of Upper Montane Forest (only ~5 km^2) are found on Doi Inthanon, Thailand's highest mountain (2,565 m) in the Thanon Thongchai range, and a smaller patch near the summit of the second highest mountain, Doi Phahompok (2,288m) in the Den Lao range. The summit zone of Doi Inthanon is well known for its rare and endemic biota, and there are, for example, many insect species known, more or less, only from there, or which are at the southern extremity of their ranges, including, for example, Coleoptera (de Rougemont, 2003), Collembola (Bedos and Deharveng, 1994), Plecoptera (Sivec and Stark, 2010) and Diptera (Hippa, 2011; Takaoka et al., 2013). The Empidoidea fauna of Doi Inthanon is exceptionally rich and important; for example, the family Brachystomatidae in Thailand, is entirely confined to the upper slopes of the mountain (Plant, 2009a; 2010a) and several genera of Hybotidae are local endemics, restricted to the upper forests of the peak (Grootaert and Shamshev, 2009; Plant et al., 2019). Recent taxonomic revisions (e.g. Plant, 2009b; 2010b; 2013; 2015) have identified numerous species of Empididae and Hybotidae restricted to high elevation habitats on Doi Inthanon which is clearly a 'hot-spot' of empidoid diversity and endemism (Plant, 2009c). Apart from remarkable endemism, another striking feature of high elevation *MHE* communities on Doi Inthanon is that many species are extraordinarily abundant (Chatelain et al., 2018; Plant et al., 2011, 2019; Sinclair and Plant, 2017). The species abundance distribution curves of *EM* and *DL* communities are similar but that of *MHE* is of very different form and *MHE* communities are characteristically uneven with high dominance and have fewer numerically rare species compared to lower *EM* and *DL* communities (Plant et al., 2019). *MHE* communities are phylogenetically richer and also have a higher proportion of taxa considered to be of Palaearctic rather than Oriental origin. Interestingly, the temporal turnover of community composition is slower (seasonality is relaxed) compared with lower elevation communities. Biodiversity, or at least that of Empidoidea, is structured very differently in *MHE* compared with *EM* and *DL* communities.

While there can be no doubt that the Upper Montane Forests of Doi Inthanon with their associated *MHE* Empidoidea communities are of exceptional interest and conservation importance, the question remains, are other Upper Montane Forests in northern Thailand equally striking? Do they warrant the particular attention deserved by those on Doi Inthanon? Can we apply the description of diversity characteristics of *MHE* Diptera communities across other Upper Montane Forests? To what extent does species composition turnover (β-diversity) across different representatives of this forest type? Given that Upper Montane Forests occur as widely dispersed patches on mountain peaks that are separated from each other by extensive lowlands, should we expect high levels of β-diversity with rich endemism amongst the communities of each isolated Upper Montane Forest patch?

The Empidoidea inhabiting Upper Montane Forest of Doi Phahompok have been poorly surveyed compared with those on Doi Inthanon and although species of Hybotidae apparently endemic to the mountain have been reported (Plant, 2013) and the previously mentioned taxonomic revisions indicate a potentially species-rich empidoid fauna. Analysis of the distribution of endemicity of the hybotid genus *Hybos* (Plant, 2013, 2014) suggested that both the Thanon Thongchai and Den Lao ranges are centres of endemism, so we might expect at least some empidoid taxa to have ranges restricted to either Doi Inthanon or Doi Phahompok. Nothing is known of how diversity is structured in Upper Montane Forest on Doi Phahompok. During 2014, we sampled Empidoidea in this habit on the summit ridge of Doi Phahompok, concomitant with a more extensive trapping program along a full elevation transect through all major forest types on Doi Inthanon. The primary objectives of the present analysis were to identify the proportion of taxa apparently endemic to either mountain and to compare how similarly diversity of Empidoidea on Doi Phahompok is structured in comparable habitats on Doi Inthanon. The results enable a better understanding of local patterns of endemism and richness providing rational support for delineating areas of conservation priority in Thailand.

MATERIALS AND METHODS

Study site

The study site on the mountain, Doi Phahompok (2,288m) is located in Chiang Mai Province, northern Thailand. Three Malaise traps were positioned in Upper Montane Forest, within 530 m horizontal distance of each other, slightly offset from the summit ridge at 2,036 m (Trap 1, 20.050417°N, 99.144056°E), 2,059 m (Trap 2, 20.052222°N, 99.142389°E) and 2,105 m (Trap 3, 20.054917°N, 99.142389°E). Traps were run throughout 2014 and serviced monthly (note all samples were lost in August, and two samples in September, probably due to interference by domestic cattle). The study site and sampling methodology at Doi Inthanon have been described previously (Plant et al., 2018; 2019). Briefly, it comprised 12 Malaise traps run along a 21.7 km long elevational transect with three traps in Lowland Deciduous Forest (one trap each at 412, 662 and 710 m), four in Lower Montane Forest (two each at 1,376 and 1,639 m) and four in Upper Montane Forest (two at 2,210 m two at 2,534 m) and one at the summit bog (2,545 m).

Taxon sorting and taxonomy

All Empidoidea were quantitatively extracted, preserved with 80% (v/v) ethanol and identified to species or morphospecies level by specialist taxonomists. The samples comprised 4,886 identified specimens from DoiPh (which were compared with 25,595 from DoiIn, Plant et al., 2019). Described genera found on either/or DoiPh and DoiIn were.- *Trichopeza* Rondani, *Brachystoma*

Mg. (Brachystomatidae). *Achelipoda* Yang, Zhang and Zhang, *Anaclastoctedon* Plant, *Chelipoda* Macq., *Hemerodromia* Mg. *Chelifera* Macq., *Dolichocephala* Macq., *Clinocera* Mg., *Empis* L., *Rhamphomyia* Zett., *Hilara* Mg., *Hormopeza* Zett. (Empididae). *Platypalpus* Macq., *Tachydromia* Mg., *Megagrapha* Melander, *Elaphropeza* Macq., *Nanodromia* Grootaert, *Stilpon* Loew, *Drapetis* Mg., *Crossopalpus* Bigot, *Hybos* Mg., *Syneches* Walker, *Syndyas* Loew, *Euhybus* Coquillett, *Ocydromia* Mg., *Oedalea* Mg., *Euthyneura* Macq. (Hybotidae). *Amblypsilotus* Bigot, *Plagiozopelma* Enderlein, *Chrysosoma* Guérin-Méneville, *Condylostylus* Bigot, *Mesorhaga* Schiner, *Systenus* Loew, *Medetera* Fischer von Waldheim, *Paramedetera* Grootaert and Meuffels, *Neurigona* Rondani, *Diaphorus* Mg., *Chrysotus* Mg., *Argyra* Macq., *Achalcus* Loew, *Lichtwardtia* Enderlain, *Hercostomus* Loew, *Paraclius* Loew, *Tachytrechus* Haliday in Walker, *Sympycnus* Loew, *Syntormon* Loew, *Chaetogonopteron* De Meijere, *Chrysotimus* Loew, *Nepalomyia* Hollis and *Acropsilus* Mik (Dolichopodidae). Hereafter, described genera are referred to without reference to their authors. Two putative undescribed genera of Dolichopodidae (designated Genus A and Genus B) and two of Hybotidae (designated Tachydromiinae Genus A and Drapetini Genus A) were found.

Statistical treatment

Data for monthly samples from DoiPh at 2,036, 2,059 and 2,105 m were routinely pooled into a single elevation class (2,036 – 2,105 m) to provide monthly and annual data on species presence and abundance on the summit ridge of DoiPh. DoiPh data were compared with DoiIn data pooled into six elevation classes (i)412+662+710m comprising *DL* Empidoidea communities in Lowland Deciduous Forest; (ii) 1,376 m and (iii) 1,639 comprising *EM* communities in the lower and upper continuum of Lower Montane Forest; (iv) 2,210 and (v) 2,534 m containing *MHE* communities in the lower and upper continuum of Upper Montane Forest forest; and (vi) samples from the DoiIn summit bog at 2,545 m. Statistical analyses and calculation of biodiversity parameters were performed in PAST (Hammer et al., 2001) as described in Plant et al. (2018). A summary explanation of the diversity measures α, D_{BP}, J, βw and k-dominance plots can be found in Magurran (2004). TePTrO index was calculated following Plant et al., 2019. It attempts to measure the relative importance of taxa with temperate Palaearctic affinities compared with those considered to have tropical Oriental affinities. Negative values of TePTrO may be indicative that community history has been strongly influenced by temperate Palaearctic faunistic elements whereas positive values may indicate that tropical Oriental influences predominate.

Abbreviations

A, abundance (number of individuals); A^*, relative abundance (abundance. trap^{-1}. month^{-1}); α, Fisher's α; D_{BP}, Berger-Parker dominance; J, equitability (employed as a measure of community evenness); βw, β-diversity *sensu* Whittaker (1960); SAD, species abundance distribution; S_{obs}, species richness; S_{P+I}, number of species common to DoiPh and DoiIn; S_{PO}, number of species found only on DoiPh; TePTrO, TePTrO Index (Temperate Palaearctic: Tropical Oriental Index). Doi Phahompok and Doi Inthanon are abbreviated as DoiPh and DoiIn respectively. Abbreviations for the *Empidoidea communities* identified by Plant et al. (2019) are italicized as *MHE* (Moist Hill Evergreen), *EM* (Mid Elevation Evergreen) and *DL* (Dry Lowland).

RESULTS

A total of 511 species of Empidoidea were collected on either/or DoiPh and DoiIn. The combined DoiPh (2,036+2,059 +2,105 m) samples contained 157 species (4,886 individuals) whereas combined samples from all elevations on DoiIn had 458 species (25,595 individuals). On DoiPh, S_{obs} in each family (with % of total in brackets) was Empididae 19 (12%), Hybotidae 92 (59%) and Dolichopodidae 46 (29%). Brachystomatidae were not found on DoiPh. Moreover 52 species were only found (S_{PO}) on DoiPh (Empididae, 5; Hybotidae, 34; Dolichopodidae, 13) and 105 species were found on both (S_{P+I}) DoiPh and DoiIn (Empididae, 14; Hybotidae, 58; Dolichopodidae, 33). Therefore approximately 33% of Empidoidea sampled on the summit of DoiPh did not occur on DoiIn (the inverse calculation, how many species were confined to DoiIn, is not helpful as sampling on DoiIn encompassed a much greater range of elevations/habitats that were not examined on DoiPh).

Table 1 reveals that the Empidoidea communities on the summit ridge of DoiPh at 2,036 – 2,105 m shared the greatest number and proportion of species with those at 1,639 m on DoiIn rather than at comparable, higher elevations. Table 1 also compares βw between DoiPh at 2,036 – 2,105 m and different elevations on DoiIn revealing higher values (increased turnover, decreasing similarity of community composition) at elevations above 2,210 and below 1,639 m. Similarity was contributed by all three empidoid families present, Empididae, Dolichopodidae and Hybotidae (Fig. 1) but different contributions to similarity occurred at genus-level (Table 2).

TABLE 1. Comparison of abundance and diversity parameters of Empidoidea communities on DoiPh with those at different elevations on DoiIn. Numbers in the sample column indicate the elevation (m) of samples that were pooled (with the number of Malaise traps used in brackets). Abbreviations.- A, abundance (number of individuals); A*, relative abundance (abundance. trap^{-1}. month^{-1}); α, Fisher's α; D_{BP}, Berger-Parker dominance; J, equitability; S_{P+I}, number of species common to both DoiPh and each separate elevation class on DoiIn (with similarity expressed in parenthesis as % of total species richness in the compared samples); S_{obs}, number of species; βw, Whittaker's measure of *β-diversity;* TePTrO, TePTrO index. Values of α, D_{BP}, J and TePTrO index for DoiIn samples were recalculated using data in Plant et al., 2019.

Sample	S_{obs}	A	A*	S_{P+I} (%)	α	D_{BP}	J	βw	*TePTrO* index
Doi Phahompok									
2036+2059+2105 (3)	157	4886	135.7	-	31.0	0.258	0.657	0.000	0.05
Doi Inthanon									
412/662/710 (3)	176	1593	49.8	31 (15.0)	50.6	0.120	0.800	0.832	+0.82
1376 (2)	142	1004	41.8	44 (20.0)	45.1	0.072	0.843	0.766	+0.10
1639 (2)	216	4190	174.6	58 (25.0)	48.3	0.142	0.751	0.614	-0.01
2210 (2)	132	5788	241.2	73 (24.3)	24.1	0.167	0.669	0.605	-0.49
2534 (2)	104	7635	318.1	35 (13.3)	17.0	0.441	0.545	0.688	-0.91
2545 (1)	81	5386	448.8	28 (9.2)	13.5	0.235	0.649	0.739	-1.11

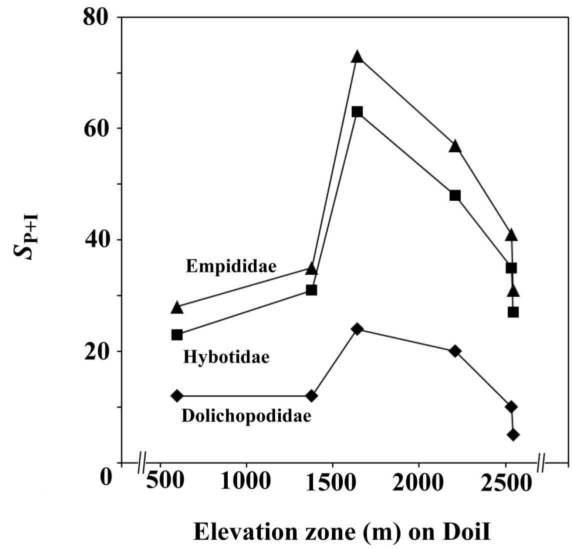

FIGURE 1. Number of species shared (S_{P+I}) between the summit area of Doi Phahompok at 2,036 – 2105 m and different elevation zones on Doi Inthanon (412 – 710, 1,376, 1,639, 2,210, 2,534 and 2,545 m). The different contributions to S_{P+I} made by Dolichopodidae, Hybotidae and Empididae are shown additively for each elevation zone.

For example, the DoiPh fauna of *Elaphropeza*, *Medetera* and *Hilara* was most similar to that on DoiIn at 1,639 m, thereby mirroring the family-level similarity maxima, but similarity of certain other genera was greater at higher (e.g. *Platypalpus*) or lower (e.g. *Amblypsilopus*) elevations. Similarity between the summit ridge communities of DoiPh and those at different elevations on DoiIn was further compared with cluster analysis of species abundance data using Bray-Curtis similarity indices (Fig. 2). Empidoidea communities from the summit of DoiPh clustered with good support alongside those from 1,639 m on DoiIn. Similar clustering patterns were also obtained using binary data (presence or absence) using both Sørensen and Jaccard similarity indices (data not shown).

Species richness was greatest during April (S_{obs} = 86) and abundance peaked during April and May (62.5% of total annual abundance) so it is clear that adult activity of Empidoidea strongly favoured the early monsoon period on DoiPh. We have previously reported (Plant et al., 2019) that on DoiIn, there is also a secondary peak of species richness and abundance associated with the late-monsoon period. Unfortunately we were not able to determine if this was also the case on DoiPh due to loss of critical samples in August and September.

As reported previously (Plant et al., 2019), the abundance of Empidoidea increased with elevation on DoiIn and the relative abundance, *A** (a value of abundance standardised for trapping effort) on the summit ridge of DoiPh was most similar to that on DoiIn at 1,376 – 1639 m (Table 1). The species abundance distribution (SAD) was investigated using

TABLE 2. Comparison of species richness, abundance and similarity at genus level of Empidoidea communities on DoiPh with those at different elevations on DoiIn. Values of S_{obs} and A are given for each genus on DoiPh. S_{P+I} is the number of species found on DoiPh that were also found in each elevation class on DoiIn and S_{P+I} * is the number of species common to DoiPh and DoiIn (all elevation classes combined). S_{PO} is the number of species in each genus found only on DoiPh.

			S_{P+I}							
	DoiPh	DoiPh	Elevation (m) class on DoiIn							
Taxon	S_{obs}	A	**412 + 662+710**	**1376**	**1639**	**2210**	**2534**	**2545**	S_{PO}	S_{P+I}*
EMPIDIDAE										
Chelipoda	6	186	2	0	3	2	1	0	2	4
Hemerodromia	2	4	0	0	1	1	1	1	0	2
Dolichocephala	2	44	0	1	0	2	2	2	0	2
Clinocera	1	1	0	0	0	0	0	0	1	0
Empis	2	232	2	2	2	1	0	0	0	2
Hilara	6	10	1	1	4	3	2	1	2	4
Total	**19**	**477**	**5**	**4**	**10**	**9**	**6**	**4**	**5**	**14**
HYBOTIDAE										
Hybos	13	299	1	1	6	7	2	2	3	10
Syneches	3	18	0	0	0	2	0	0	1	2
Syndyas	1	1	0	0	0	0	0	0	1	0
Bicellaria	1	4	0	0	0	0	0	0	1	0
Ocydromia	1	3	0	0	1	0	1	0	0	1
Oedalea	1	7	0	0	0	0	0	0	1	0
Euthyneura	1	2	0	0	2	1	1	1	0	1
Platypalpus	22	689	6	6	11	11	11	11	5	17
Tachydromia	6	70	0	0	2	2	2	2	4	2
Megagrapha	2	2	0	0	0	1	2	2	0	2
Elaphropeza	30	869	2	7	13	3	5	3	14	17
Drapetini-Genus-A	3	28	1	1	2	1	1	1	1	1
Nanodromia	1	1	0	1	1	0	0	0	0	1
Stilpon	5	1368	1	2	1	0	0	0	2	3
Drapetis	2	11	0	1	0	0	0	0	1	1
Total	**92**	**3372**	**11**	**19**	**39**	**28**	**25**	**22**	**34**	**58**
DOLICHOPODIDAE										
Amblypsilopus	4	99	2	2	3	2	0	0	1	3
Chrysosoma	2	8	0	1	0	0	0	0	1	1
Mesorhaga	1	1	0	0	1	0	0	0	0	1
Systenus	2	5	0	0	0	0	0	0	2	0
Medetera	12	129	3	4	7	3	2	0	4	8
Neurigona	3	14	0	0	2	1	1	0	1	2
Chrysotus	1	106	1	1	0	1	0	0	0	1
Diaphorus	4	40	0	0	1	2	1	0	2	2
Chrysotimus	3	315	0	1	1	1	1	1	2	1
Hercostomus	2	227	0	0	0	2	2	2	0	2
Sympycnus	7	27	3	2	6	6	2	1	1	6
Chaetogonopteron	2	11	1	1	2	1	0	0	0	2
Nepalomyia	3	55	2	0	1	1	1	1	0	3
Total	**46**	**1037**	**12**	**12**	**24**	**20**	**10**	**5**	**14**	**32**
Grand total	**157**	**4886**	**28**	**35**	**73**	**57**	**41**	**31**	**53**	**104**

k-dominance plots (Fig. 3) revealing that the SAD of empidoid communities from the summit of DoiPh (at 2,036 – 2,105 m) more closely matched that of DoiIn communities at 2,200 m than at other elevations on DoiIn. The SAD of Empidoidea communities on DoiIn suggests that they become increasingly dominated by a few abundant

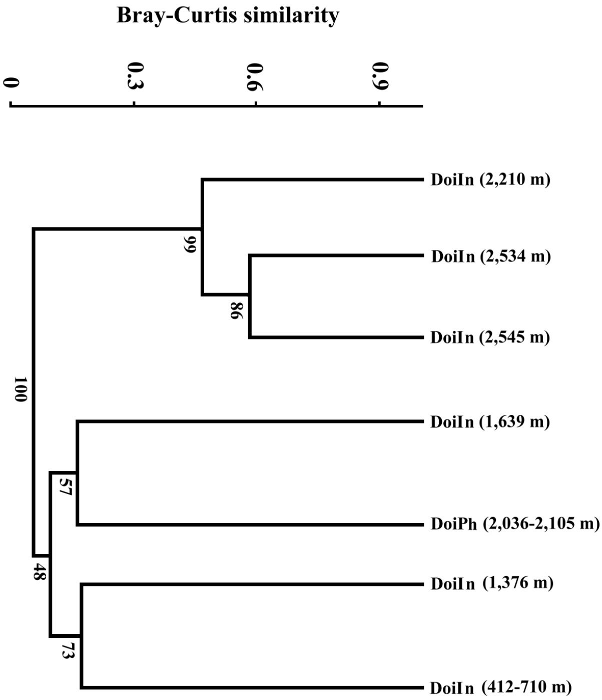

FIGURE 2. Cluster analysis of Empidoidea communities from the summit of Doi Phahompok.- (DoiPh 2,036 – 2,105 m) and different elevation zones on Doi Inthanon.- DoiIn (412 – 710 m), DoiIn (1,376 m), DoiIn (1,639 m), DoiIn (2,210 m), DoiIn (2,534 m) and DoiIn (2,545 m) using unweighted pair-group average and Bray-Curtis similarity indices. Bootstrapping was performed with 1,000 resamples; the percentage of replicates where each node is still supported is shown.

species at higher elevations and indeed at higher elevations, the populations are less even (lower values of *J*) and have high dominance (higher values of D_{BP}). Comparison of values of *J* and D_{BP} of summit communities on the two mountains (Table 1) suggests that those on the summit of DoiPh are most similar to those on DoiIn at 2,210 and 2210 – 2334 m respectively. Comparison of values of Fisher's α (which provides a robust means of measuring overall diversity) indicates that diversity on the summit of DoiPh most closely matches that on DoiIn at 1,639 – 2,210 m (Table 1). The value of TePTrO index (0.05, Table 1) is tentatively considered to imply that the proportion of species on DoiPh having putative Oriental or Palaearctic origins is similar to that on DoiIn at 1,639 m.

DISCUSSION

Endemism

The finding that 33% of the Empidoidea present on the summit ridge of DoiPh were not present at any elevation/habitat on DoiIn indicates high turnover of species composition (β-diversity). It also suggests that DoiPh has a high proportion of locally endemic species and supports the conclusion of Plant (2013, 2014) that the mountain (and

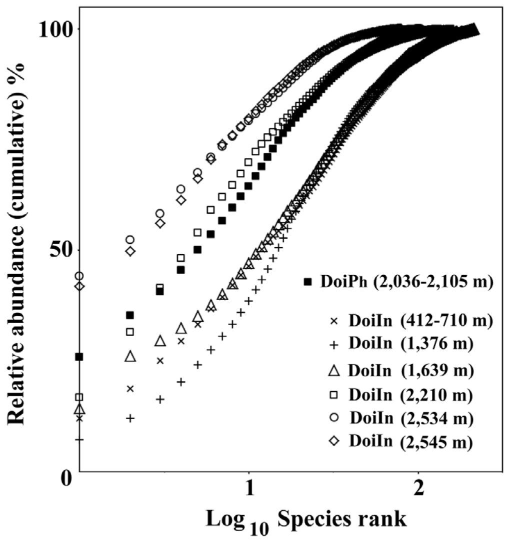

FIGURE 3. K-dominance plot of species abundance distribution of Empidoidea from the summit of Doi Phahompok.- DoiPh (2,036 – 2,105 m) and different elevation zones on Doi Inthanon.- DoiIn (412 – 710 m), DoiIn (1,376 m), DoiIn (1,639 m), DoiIn (2,210 m), DoiIn (2,534 m) and DoiIn (2,545 m). The relative cumulative abundance (%) is plotted against $\log_{10}$ species rank (from highest to lowest).

Den Lao range of which it is part) is a significant centre of endemism. The high elevation Upper Montane Forest biotopes of DoiIn and DoiPh are in effect, ecological islands, on two separate mountain ranges, separated from each other by 176 km of lower elevation terrain. Gene-flow is probably very restricted between populations within these specialised and isolated fly communities which will have diverged and developed differently from each other.

It is important to appreciate that the magnitude of endemism on DoiPh might have been overestimated due to uneven sampling effort on the two mountains (DoiIn was sampled with more Malaise traps and has been studied over many years compared to DoiPh). Also, some species present on DoiPh may yet be found on DoiIn (e.g. *Bicellaria thailandica* Barták, Plant and Kubík is an Upper Montane Forest specialist present on DoiPh and Mae Wong National Park but apparently absent from DoiIn despite that mountain being located geographically between the two others). Additionally, inter-annual differences in species composition are common in tropical forests (Bigger, 1976; Grimbacher and Stork, 2009) and are profound on DoiIn (Plant et al., 2019) such that a sampling regime restricted to one year is highly likely to underestimate species richness. Thus, that *Dolichocephala incus* Sinclair and Plant was not found on DoiPh during this study but is previously known from both DoiPh and DoiIn (Sinclair and Plant, 2017) may be an example of this problem

On DoiPh, genera such as *Chelipoda* and *Hilara* (Empididae), *Systenus* and *Medetera* (Dolichopodidae) and especially *Elaphropeza* and *Platypalpus* (Hybotidae) are conspicuous contributors to endemism (Table 2). *Chelipoda*, *Hilara* and *Platypalpus* also contribute to endemism on the upper slopes of DoiIn along with genera such as *Anaclastoctedon*, *Hybos*, *Hercostomus*, *Nepalomyia* and *Chaetogonopteron*. A rich community of Clinocerinae (Empididae) including several abundant and endemic species is characteristic of the Upper Montane Forest of DoiIn and all Thailand species of *Brachystoma* and *Trichopeza* (Brachystomatidae) are apparently endemic there.

Community similarity

How similar are communities of Empidoidea in Upper Montane Forest at 2,036 – 2,105 m on DoiPh to those on DoiIn at comparable elevations? Cluster analysis indicated comparability with somewhat lower elevations at 1,639 m on DoiIn and this was supported by values of S_{P+I} and TePTrO index. Evenness measured as *J* and k-dominance plots of SAD both suggested greatest similarity at 2,210 m, while Fisher's α indicated greatest similarity at 1,639 – 2,210 m. Values of βw also indicated greater similarity at 1,639 – 2,210 m. These six analyses support the conclusion that diversity and community characteristics on the summit of DoiPh are comparable with those of similar or somewhat lower communities on DoiIn in the range of 1,639 – 2,210 m. However, values of D_{BP} suggested a dominance structure analogous with that at 2,210 – 2,534 m whereas *A* was* most similar to that on DoiIn at 1,376 – 1,639 m.

It is concluded that, based on these similarities of species composition and hypothesised biogeographic origin of taxa, the DoiPh empidoid communities at 2,036 – 2,105 m are probably more closely analogous with *EM* rather than *MHE* communities on DoiIn (occurring 1,000 – 2,000 and >2,000 m respectively on DoiIn). However the distribution of abundance, in particular the prominence of extremely abundant species (high dominance), indicates that diversity on DoiPh is structured similarly to that of *MHE* communities at comparable elevations on DoiIn. This suggests that factors driving structural diversity in favour of uneven populations at higher elevations cannot be operating at the level of the taxon (or indeed functional traits associated with it) but are more likely to be general adaptive responses to conditions at higher elevation.

Certain very abundant species made large contributions to high dominance at high elevation on both mountains. (e.g. various species of *Chelipoda*, *Platypalpus*, *Medetera*, *Hercostomus* and *Nepalomyia*). However, there were many more species that were found to be extremely abundant at >2,200 m on DoiIn (Plant et al., 2019) but which were absent or infrequent at 2,036 – 2,105 m on DoiPh. Prominent amongst these were several species of *Clinocera* and *Dolichocephala* but genera such as *Chelipoda*, *Hilara*, *Megagrapha*, *Chrysotimus*, *Sympycnus* and *Chaetogonopteron* also contributed. Conversely, species contributing greatly to dominance on DoiPh but infrequent or absent above 2,200 m on DoiIn included species of *Chelipoda*, *Empis*, *Hybos*, *Chrysotimus*, *Elaphropeza* and *Stilpon*. There are no obvious patterns to how dominance is distributed amongst taxa except that many of these genera that include at least some very abundant species are restricted to, or more species rich, at higher elevations in Thailand (e.g. *Chelipoda*, *Clinocera*, *Dolichocephala*, *Hilara*, *Megagrapha*, *Platypalpus*, *Hercostomus*) (see Plant et al., 2019 for detailed evaluation of their habitat/elevation ranges). *Elaphropeza* is a highly speciose hybotid genus preferentially inhabiting lowland in

Thailand (Plant et al., 2011) and Plant et al (2019) found that all but eight of the 59 species recorded from DoiIn occurred at mid to low elevations. Thus the present finding of 30 species of the genus at 2,036 – 2,105 m on DoiPh is perhaps a little surprising, although it is entirely consistent with the conclusion advanced above, that the composition of DoiPh high elevation communities better corresponds with that at somewhat lower elevation elsewhere. A few species of *Elaphropeza* also contributed to high dominance in the DoiPh sample whereas on DoiIn the SAD was more even with few abundant species and many rare ones.

Concluding remarks

The Empidoidea communities inhabiting Upper Montane Forest around the summit of DoiPh are more closely analogous with the extremely diverse assemblages of species occurring at somewhat lower elevations on DoiIn. The descriptions of Empidoidea communities in the main forest habitat types of DoiIn do appear to be scalable over larger geographic areas as suggested by Plant et al. (2019) even 'though β-diversity (species turnover with distance) effects change the actual species composition. It should be noted particularly that DoiPh supports numerous unique (endemic) species not found on DoiIn and is of very substantial conservation interest. Indeed, we suspect high levels of β-diversity with rich endemism are characteristic of the widely dispersed patches of Upper Montane Forest in northern Thailand and the habitat is surely of utmost conservation concern, wherever it occurs. This work also reaffirms the unique nature of high elevation upper Upper Montane Forest on Doi Inthanon, above approximately 2,200 m. This habitat and the Empidoidea communities associated with it are *not* found anywhere else. Doi Phahompok (and other mountains in Thailand) are simply not high enough to support them. The summit slopes of Doi Inthanon are distinctive, unique and vital havens of biodiversity.

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