

Spatiotemporal dynamics of insect diversity in tropical seasonal forests is linked to season and elevation, a case from northern Thailand

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Abstract. Seasonal forests with alternating wet and dry seasons are geographically predominant in the tropics but little is known of the spatiotemporal dynamics of the megadiverse insect communities inhabiting them. We studied variation in diversity and abundance parameters of two taxonomically and functionally distinct insect orders, Diptera and Auchenorrhyncha throughout 12 months across a 2,100 m elevation gradient in seasonal forests in northern Thailand. The interactions of space (elevation) and time (successive months of the year) on species richness, abundance, evenness and local community turnover were interpreted on spatiotemporal grids. We found that: (1) The spatiotemporal dynamics of diversity parameters are taxon-dependent. (2) Diversity of Diptera and Auchenorrhyncha broadly correlates with monsoon rains despite taxonomic and functional dissimilarity. (3) Peak diversity and abundance of Diptera and Auchenorrhyncha occurred at different elevations and for different durations during the wet season but with bimodal peaks coinciding with early- and late-monsoon periods. (4) Species-rich early-monsoon assemblages had greater evenness than relatively depauperate late-monsoon assemblages. (5) Higher elevation assemblages have greater temporal stability suggesting that they are less seasonally constrained than low-elevation assemblages; they had proportionally more species with longer activity periods. Our results emphasise that seasonality is an under-recognised variable in insect diversity studies and since diversity and its structure are closely linked to climatic seasonality in globally extensive tropical seasonal forests, any assessment of global biodiversity by extrapolation from local and regional measurements requires that seasonal patterns be recognised.

Key words. Auchenorrhyncha, Diptera, diversity, insect, spatiotemporal dynamics, seasonality, tropical seasonal forest

INTRODUCTION

Mega-diverse insect assemblages contribute greatly to the outstandingly rich biodiversity of tropical forests. Knowledge of the spatial and temporal patterns of insect diversity and assemblage composition is fundamental to understanding the ecological processes operating in tropical forests. Furthermore, since assessment of biodiversity at a global scale inevitably involves extrapolation from smaller spatiotemporal sampling units (Colwell & Coddington, 1994) description of spatiotemporal distributions of taxa and functional groups is an essential first step in the quantitative evaluation of global

diversity (Basset et al., 2015). Spatial patterns of species richness within small areas (α -diversity) and species turnover between areas (β -diversity) have been extensively studied in tropical biotopes, especially in respect of environmental gradients (Rahbek, 2005; Gardner et al., 2010; Peters et al., 2016). However, temporal responses to intra-annual seasonal changes or longer inter-annual variations and interactions between elevation and seasonality remain less well known (Murphy & Lugo, 1986; Novotny, 1993; Grimbacher & Stork, 2009; Valtonen et al., 2013; Basset et al., 2015). Tropical forests may be broadly categorised (Murphy & Lugo, 1986) as an equatorial belt of relatively aseasonal ‘everwet’ forest (equatorial rainforest) which becomes increasingly subject to longer and more intense dry periods at progressively higher latitudes (moist deciduous, semi-evergreen, tropical mixed, tropical dry, and monsoon forests) although seasonality may be relaxed locally on tropical mountains (Doumenge et al., 1995; Plant, 2009). While seasonality is slight in everwet forest (Walter & Lieth, 1967; Murphy & Lugo, 1986) it can be extreme in forests that experience prolonged dry seasons where it may be an important driver of α - and β -diversity amongst plants, influencing many aspects of life history such as leafing, flowering, fruiting and vegetation structure (van Schaik et al., 1993; Davidar et al., 2005; Davidar et al., 2007). Flushing and flowering in water stressed seasonally dry forests often occur around the start of the rainy season (van Schaik et al., 1993). However, leaf exchange patterns can be complex (Williams et al., 2008) and vegetative phenology

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may become disengaged from direct correlation with rainfall with leafing during the dry season reliant more upon subsoil water reserves (Borchert, 1999; Elliot et al., 2006).

Various studies have shown that insect abundance is also greatest at the start or during the rainy season (Wolda, 1978a; Frith & Frith, 1990; Hill, 1993; Novotny & Basset, 1998; DeVries & Walla, 2001; Wiwatwitaya & Takeda, 2005; Plant et al., 2011), often coincident with leaf flush and flowering (Basset, 1991; Kato et al., 1995; Richards & Coley, 2007) although other phenological profiles have been reported (Buskirk & Buskirk, 1976; Boinski & Fowler, 1989; Hill et al., 2003; Plant et al., 2011), and responsiveness to seasons can also be influenced through modification of microclimate by vegetation structure (Janzen, 1973; Shapiro & Pickering, 2000; Richards & Windsor, 2007), ecological groups (Grimbacher et al., 2008; Grimbacher & Stork, 2009; Molleman et al., 2016), taxonomic level and body size (Smythe, 1982; Ribeiro & Freitas, 2011). Tropical insects clearly demonstrate a wide range of seasonal patterns, even at the same site (Wolda, 1988; Grimbacher & Stork, 2009; Kishimoto-Tamada & Itioka, 2015). The misconception identified by Barlow & Woiwod (1989), that insect abundance is less seasonal in tropical forests than in temperate habitats remains widespread and is particularly unfortunate as ~75% of tropical forest experiences profound seasonality (Murphy & Lugo, 1986).

Wolda (1978a, b) hypothesised that insect populations of seasonal forests should fluctuate more than in climatically stable habitats and that their abundance should be directly related to seasonal variations in the abundance of food resources. An increase in net primary productivity linked to rainfall, temperature and irradiance should cascade through the food chain triggering responses at higher trophic levels. Climate-driven environmental effects probably also underlie the varied profiles of diversity and abundance reported along elevation gradients (Dunn et al., 2007; Beck et al., 2011; Beck et al., 2017) but interactions between seasonality and elevation remain largely unexplored. As yet, we have no clear and consistent answers to questions such as when and for how long insects are active in seasonal forests and if activity is correlated with seasonality. If species diversity varies with season, how does its composition turnover with respect to time and does the structure of assemblages (their evenness, dominance etc.) also change? Are seasonal responses modified by elevation and do phenological traits differ between trophic levels, functional groups, taxonomic position, phylogenetic or climate history? Resolving these questions will inform a better understanding of the spatiotemporal dynamics and diversity of insect assemblages in tropical forests.

In this study, we examine the species richness, abundance, turnover patterns, and seasonal phenology of two diverse insect orders, Auchenorrhyncha and Diptera, throughout a complete year along a 412–2,534 m elevation gradient in a monsoon forest in northern Thailand. The vegetation and local climate of the survey area at Doi Inthanon (18°35'N, 98°29'E) are well known (Bedos, 1994; Hara et al., 2002;

Teejuntuk et al., 2002; Kanzaki et al., 2004; Chatelain et al., 2018) and are probably representative of the widespread succession pattern of the northern Thailand region (Santisuk, 1988). The lower slopes (approximately <1,000 m) support dry-dipterocarp and mixed deciduous-evergreen forests which experience a severe 6–7 month dry season with >90% of annual rainfall of 800–1,500 mm occurring between June and October with dry and wet season temperatures averaging ~20°C and ~25°C respectively. Above 1,000 m, evergreen influence increases with successively, dry evergreen, hill evergreen, moist hill evergreen forest and areas of *Rhododendron* and *Sphagnum* bog at the summit (2,545 m). The summit experiences >90% of annual rainfall of 2,000–3,000 mm between May and October and a mean annual temperature of 12.9°C with ground frost occurring on about 10 days per year (data calculated by ARP from meteorological records collected at the summit from 2004–2014). Whereas seasonality imposed by the monsoon is experienced at all elevations on Doi Inthanon, its intensity (especially in regard of precipitation and temperature) is modified by elevation and the site provides an opportunity to examine seasonal and elevational responses of structural diversity to these changes.

Auchenorrhyncha are primary consumers, phytophagous sap-feeders or fungivores on the aerial parts of their host plant(s) whereas the families of Diptera studied here are predominantly secondary consumers with predatory immature stages inhabiting soils and decaying organic matter; adults may be predatory and/or nectivorous. The target taxa are thus not only taxonomically distinct but also trophically dissimilar and furthermore, they generally utilise different habitat elements within the various forest biotopes. Our objective was to identify differences and commonalities in the spatiotemporal patterns of taxon richness, abundance, taxon turnover and the evenness of assemblages of Diptera and Auchenorrhyncha and investigate if seasonal relaxation at higher elevations linked to elevated precipitation might broaden their phenological profiles. We stress that estimations of insect biodiversity in tropical seasonal forests are sensitive to the spatiotemporal dynamics of the taxonomic and functional groups involved.

MATERIAL AND METHODS

Taxa studied and sampling site. We studied seven families of Diptera and 18 families of Auchenorrhyncha (Table 1) extracted from trap samples. Insects were sampled at Doi Inthanon National Park, Chiang Mai Province, Thailand using Malaise traps positioned along an elevation and habitat succession gradient between 412 m (18.4992°N, 98.6683°E) and 2545 m (18.5889°N, 98.4847°E). Number of traps and predominant forest types at each trap site on the gradient were: 412 m, 1 trap, dry dipterocarp; 662 m, 1 trap, dry evergreen; 710 m, 1 trap, dry evergreen; 1,376 m, 2 traps, mixed deciduous, lower hill evergreen with some *Pinus*; 1,639 m, 2 traps, hill evergreen; 2,210 m, 2 traps, moist hill evergreen; 2,534 m, 2 traps, upper moist hill evergreen; 2,545 m, 1 trap, *Rhododendron* scrub with adjacent *Sphagnum* bog and upper moist hill evergreen forest. Traps were operated

Table 1. Species richness (S_{obs}) and abundance (A) of Diptera and Auchenorrhyncha families trapped over 12 months sampling at Doi Inthanon in 2014.

Order	Family	Species richness (S_{obs})	Abundance (A)
Diptera	Brachystomatidae	3	66
	Empididae	72	9185
	Hybotidae	203	7567
	Dolichopodidae	179	8777
	Stratiomyidae	49	441
	Syrphidae	23	221
	Therevidae	1	1
Auchenorrhyncha	Cicadidae	2	4
	Membracidae	16	67
	Machaerotidae	4	13
	Cercopidae	13	55
	Aphrophoridae	9	56
	Achilidae	8	141
	Caliscelidae	2	6
	Cixiidae	16	326
	Delphacidae	19	1137
	Derbidae	19	84
	Eurybrachidae	1	1
	Flatidae	2	3
	Fulgoridae	1	1
	Issidae	15	233
	Lophopidae	1	6
	Meenoplidae	7	93
	Trophiduchidae	4	16
	Nogodinidae	1	10

from the start of January until the end of December 2014 (data for January and February at 412, 662 and 710 m were lost due to human disturbance of traps). Traps were emptied monthly at the end of each calendar month and target taxa identified to species or morphospecies (hereafter referred to as 'species') and numbers of individuals of each taxon counted. Insects were preserved in 80% (v/v) ethanol in the collections of Queen Sirikit Botanic Garden, Entomology Section, Mae Rim, Chiang Mai, Thailand.

Diversity and turnover. Data of species richness (S_{obs}) and abundance (A) from monthly Malaise trap samples were routinely pooled into six elevation zones (<500, 500–1,000, 1,000–1,500, 1,500–2,000, 2,000–2,500 and >2,500 m) reflecting vegetation transitions summarised above. Because different numbers of traps were operated in different elevation zones, abundance was standardised against trapping effort as Relative Abundance, A^* (abundance. trap $^{-1}$. month $^{-1}$). Univariate statistics, Berger-Parker dominance (D_{BP}), Equitability (J) and estimation of total diversity (S_{est}) from the proportion of singleton and doubleton species using Chao-1 or by individual rarefaction followed by fitting to the so-called Michaelis-Menton (rectangular hyperbolic) saturation model (Magurran, 2004), were performed in PAST version 3.0 (Hammer et al., 2001). For measurement of species turnover through elevation and time we represented the data as a grid of elevation zones and months. Turnover between a focal quadrat of the grid and

any other was then calculated as Whittaker's measure, β_w (Whittaker, 1960) in PAST; $\beta_w = (S\bar{\alpha}) - 1$ where S is the total number of species recorded from both quadrats and $\bar{\alpha}$ is the average number of species found within the quadrats. While β_w provides a good measure of turnover between adjacent quadrats in the grid, it is additive and tends to assume extreme values when the differences in the richness between the focal and the neighbouring quadrat are large, as might be expected if the other quadrat is more distant from the focal quadrat (Koleff et al., 2003). In order to assess more accurately how turnover changed locally within the grid we employed two measures: Mean Local Turnover (β_{wL}) and Mean Monthly Turnover (β_{wM}). For calculation of β_{wL} , values of β_w for all quadrats temporally and altitudinally adjacent to the focus quadrat were found and averaged (thus if the focus quadrat is 1,500–2,000 m in May, β_{wL} is the mean of values obtained for 1,500–2,000 m in April and June; 2,000–2,500 in April, May & June and 1,000–1,500 in April, May & June). For any elevation zone, β_{wM} was calculated as the mean value of the month before and after the focus month (thus if the focus quadrat is 1,000–1,500 in September, β_{wM} is the average value of β_w for August and October at the same elevation). Calculations of β_{wL} and β_{wM} were iterated for every quadrat in the grid. Diversity, abundance and turnover parameters were visualised as contour maps on the elevation/month grid using the multiquadric gridding algorithm in the gridding module of PAST.

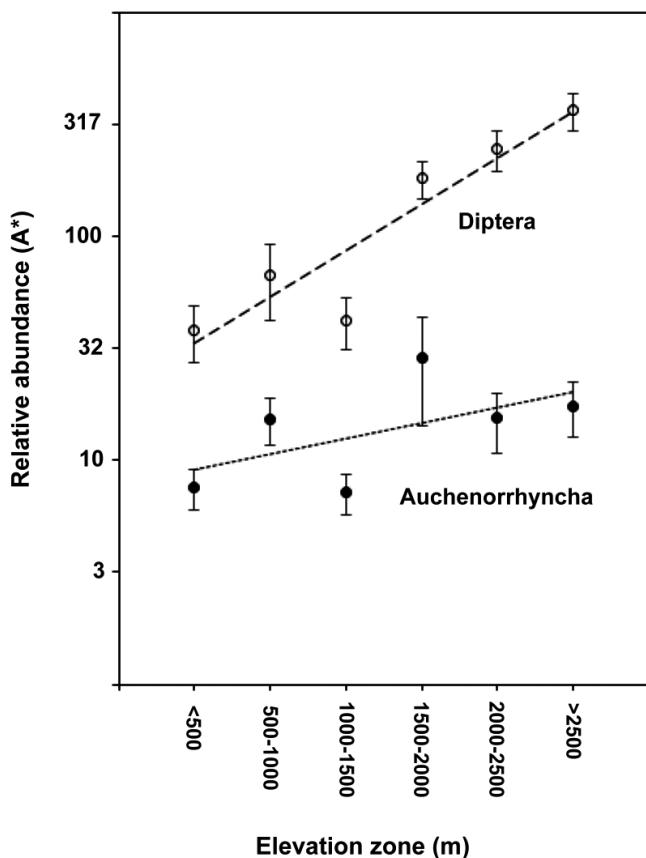


Fig. 1. Relative abundance, A^* (number of individuals caught trap $^{-1}$ month $^{-1}$) of Diptera and Auchenorrhyncha trapped in six elevation zones over 12 months sampling at Doi Inthanon in 2014. Standard errors indicated. Note log₁₀ scale. Data were fitted to a linear regression model in PAST; Diptera, open circles ($r^2 = 0.8567, p = 0.0081$); Auchenorrhyncha, closed circles ($r^2 = 0.3182, p = 0.2434$). In Kruskal-Wallis H -tests of untransformed data there was a significant difference between the medians for Diptera ($H = 29.3, p < 0.01$) but not for Auchenorrhyncha ($H = 3.3, p = 0.657$).

Seasonality. We compared five parameters to quantify seasonality in different elevation zones. (1) SM , the mean of the total number of months in which each species was recorded. (2) $SM_{>6}$, the number of species with $SM > 6$ months expressed as a percentage of the total number of species recorded throughout the year at each elevation. (3) SL , the length of season, was calculated by subtracting the total number of months before the first and after the last monthly occurrence from 12 (the total number of months in a year). (4) $SL_{>6}$, the number of species with $SL > 6$ months expressed as a percentage of the total number of species recorded throughout the year at each elevation. (5) L_e , seasonality of each species was quantified by measuring variance standardised with respect to the mean of its distribution amongst 12 one-month periods for each species using Lloyd's Index (L_i):

$$L_i = \frac{s^2 - x}{x^2}$$

Where s^2 is the variance and x is the mean (Novotny & Basset, 1998). The value L_e was then calculated as the mean value of L_i for all species occurring at a particular elevation. We also crudely estimated the incidence of multivoltine species by inspection of the abundance phenology of individual

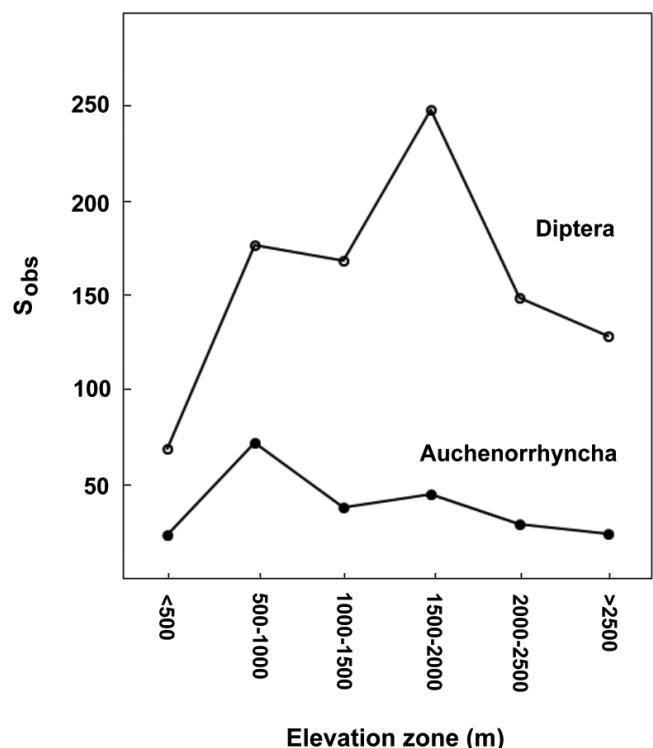


Fig. 2. Observed species richness (S_{obs}) of Diptera and Auchenorrhyncha trapped in six elevation zones over 12 months sampling at Doi Inthanon in 2014. Diptera, open circles; Auchenorrhyncha, closed circles.). In Kruskal-Wallis H -tests there was a significant difference between the medians for Diptera ($H = 22.1, p < 0.01$) and Auchenorrhyncha ($H = 14.3, p < 0.05$).

species. A species was considered bivoltine or multivoltine if two or more distinct abundance maxima occurred, separated by a period of two or more months with low abundance or absence (species with annual totals of <10 individuals were excluded).

RESULTS

Species richness and abundance. A total of 531 species (26,249 individuals) of Diptera and 140 species (2,252 individuals) of Auchenorrhyncha were recognised and analysed (Table 1). Estimates of total diversity (S_{est}) using Chao-1 and individual rarefaction respectively were 662 and 572 (Diptera), 176 and 173 (Auchenorrhyncha) suggesting that we observed ~80–90 % of actual diversity. Relative abundance (A^*) of both Auchenorrhyncha and Diptera increased with elevation (Fig. 1). Although overall species richness (S_{obs}) of Diptera was maximal at ~1,500–2,000 m and that of Auchenorrhyncha at ~500–1,000 m (Fig. 2), it should be noted that sampling effort was not uniform along the elevation gradient. The richness and identity of taxa caught with malaise traps is not scalable to trapping effort and values of species richness cannot be normalised in the same way as abundance data are herein. Relative abundance of both orders was bimodal with peak abundances in March–June and September–October (Fig. 3). Species richness was maximal between April and June (Fig. 4) with a later secondary peak of S_{obs} later in the year October–November (Diptera) and possibly a smaller secondary peak for Auchenorrhyncha during September.

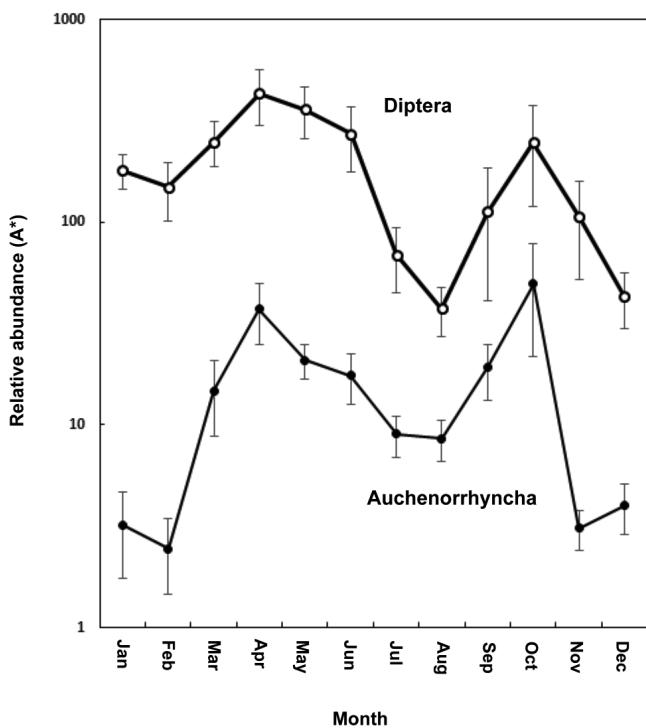


Fig. 3. Relative abundance, A^* (number of individuals caught. trap $^{-1}$. month $^{-1}$) of Diptera and Auchenorrhyncha over 12 months sampling at Doi Inthanon in 2014. Standard errors indicated. Note log₁₀ scale. In Kruskal-Wallis H -tests of untransformed data there was a significant difference between the medians for Diptera ($H = 24.5$, $p < 0.05$) and Auchenorrhyncha ($H = 34.3$, $p < 0.01$).

The interactions of space (elevation) and time (successive months of the year) on abundance of Diptera and Auchenorrhyncha are shown in Fig. 5A and 5C respectively. Diptera abundance was low at elevations $< 1,500$ m throughout the year and they were exceptionally abundant at $> 2,000$ m during the early monsoon period in April and May with a secondary peak in October at the end of the monsoon (Fig. 5A). Auchenorrhyncha abundance was skewed far less in favour of higher elevations with peak abundances associated with May–June at 500–1,500 m, April–May at $> 2,000$ m and a later mid-elevation peak at 1,000–2,500 m during September and October (Fig. 5C). Gridding of S_{obs} with respect to elevation and month illustrates that α -diversity increased progressively at upper mid-elevations from January to a peak in April–May extending across all elevations above $\sim 1,000$ m, but was greatest at 1,500–2,000 m (Fig. 5B); species richness declined sharply thereafter during mid-monsoon from June onwards with only a minor peak in S_{obs} at the end of the monsoon/start of cold dry season during October–December. Maximal species richness of Auchenorrhyncha occurred at lower elevations than in Diptera (500–1,000 m) but was more equably spread throughout the monsoon season between March and September (Fig. 5D). The May–June peak in α -diversity extended upwards above 1,000 m but occurred slightly earlier at higher elevations and there was a small late monsoon peak during September and October at 1,500–2,500 m.

Equitability (J) provides a measure of the evenness with which individuals are divided amongst the taxa present; $J =$

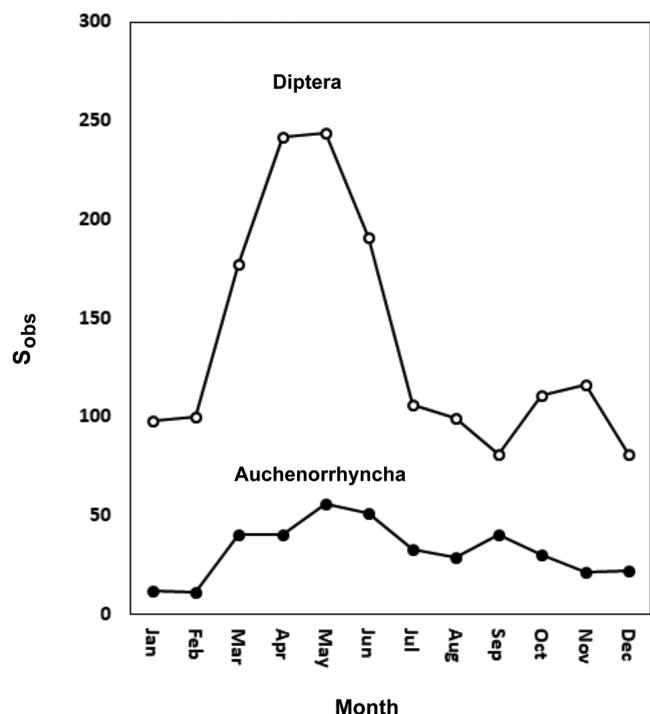


Fig. 4. Observed species richness (S_{obs}) of Diptera and Auchenorrhyncha over 12 months sampling at Doi Inthanon in 2014. Diptera, open circles; Auchenorrhyncha, closed circles. In Kruskal-Wallis H -tests there was a significant difference between the medians for Diptera ($H = 32.4$, $p < 0.01$) and Auchenorrhyncha ($H = 24.4$, $p < 0.05$).

$H/\log n$, where H is the Shannon index of diversity and n is the total number of individuals. Values of J were highest for Diptera at mid-elevations (Fig. 6A) and for Auchenorrhyncha at lower elevations (Fig. 6B). Berger-Parker dominance (which measures the number of individuals of the dominant taxon relative to the total number of individuals) was negatively correlated with Equitability (Diptera, $r^2 = 0.678$, $p < 0.05$; Auchenorrhyncha, $r^2 = 0.946$, $p < 0.01$). Quadrats with high species richness in the elevation/month grid (Figs. 2, 5A, 5D) appeared to weakly correspond with those of high evenness and low dominance (Fig. 6A, B) although correlations of S_{obs} with J and D_{BP} across the six elevation zones (pooled data for all months of the year) were weak for Diptera (J ; $r^2 = 0.331$, $p = 0.232$; D_{BP} ; $r^2 = 0.292$, $p = 0.269$) and S_{obs} was uncorrelated with J or D_{BP} in Auchenorrhyncha (J ; $r^2 = 0.016$, $p = 0.813$; D_{BP} ; $r^2 = 0.023$, $p = 0.772$). It is perhaps simplistic to suppose a simple relationship between richness and evenness as the latter is clearly dependent on both elevation and season; for example, in Diptera, J is similar at all elevations during the early monsoon but is strongly depressed during the late monsoon in September and October (Fig. 7) and for Diptera, at least, the early monsoon peak of richness and abundance is characterised by a large number of species with broadly similar abundances whereas the late monsoon peak has fewer species, some of which are very abundant.

Species turnover. As species turnover measured using β_{W} affords an accurate indication of community turnover (Wilson & Shmida, 1984) it is clear that assemblage similarity of

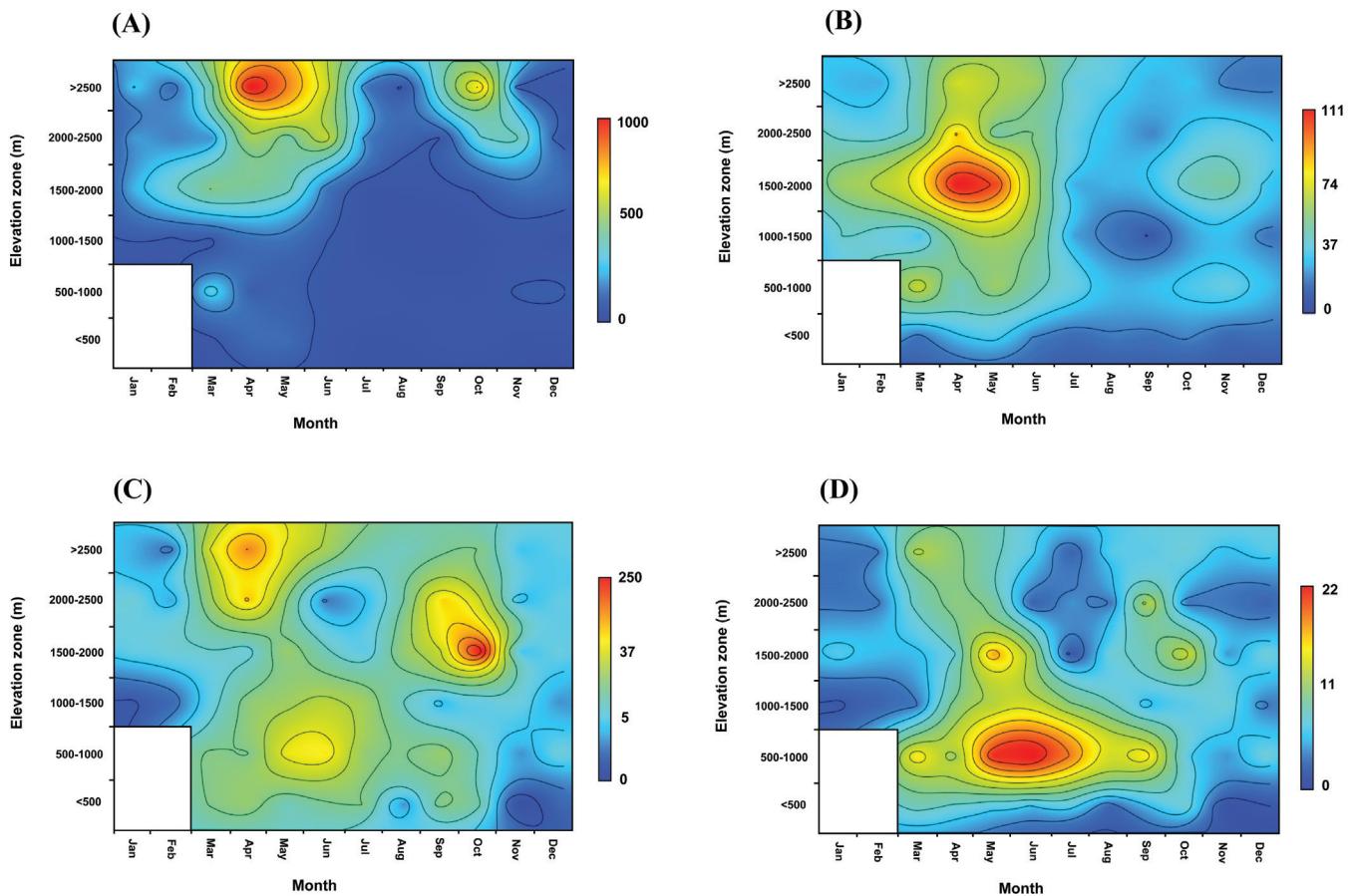


Fig. 5. Spatiotemporal variation in abundance and species richness of Diptera and Auchenorrhyncha trapped over 12 months sampling over six 500 m elevation zones at Doi Inthanon in 2014. The left panel shows Relative Abundance, A^* (number of individuals caught, trap $^{-1}$.month $^{-1}$) as $\log_{10}(1+A^*)$ for Diptera (A) and Auchenorrhyncha (C). The right panel shows observed species richness, S_{obs} , for Diptera (B) and Auchenorrhyncha (D). Data were plotted on a grid of elevation zone (vertical axis) and months (horizontal axis) and mapped using the multiquadric gridding algorithm in the gridding module of PAST. Values of $\log_{10}(1+A^*)$ and S_{obs} are indicated by the colour scale bars. Data are not available for January and February at <500 m and 500–1,000 m.

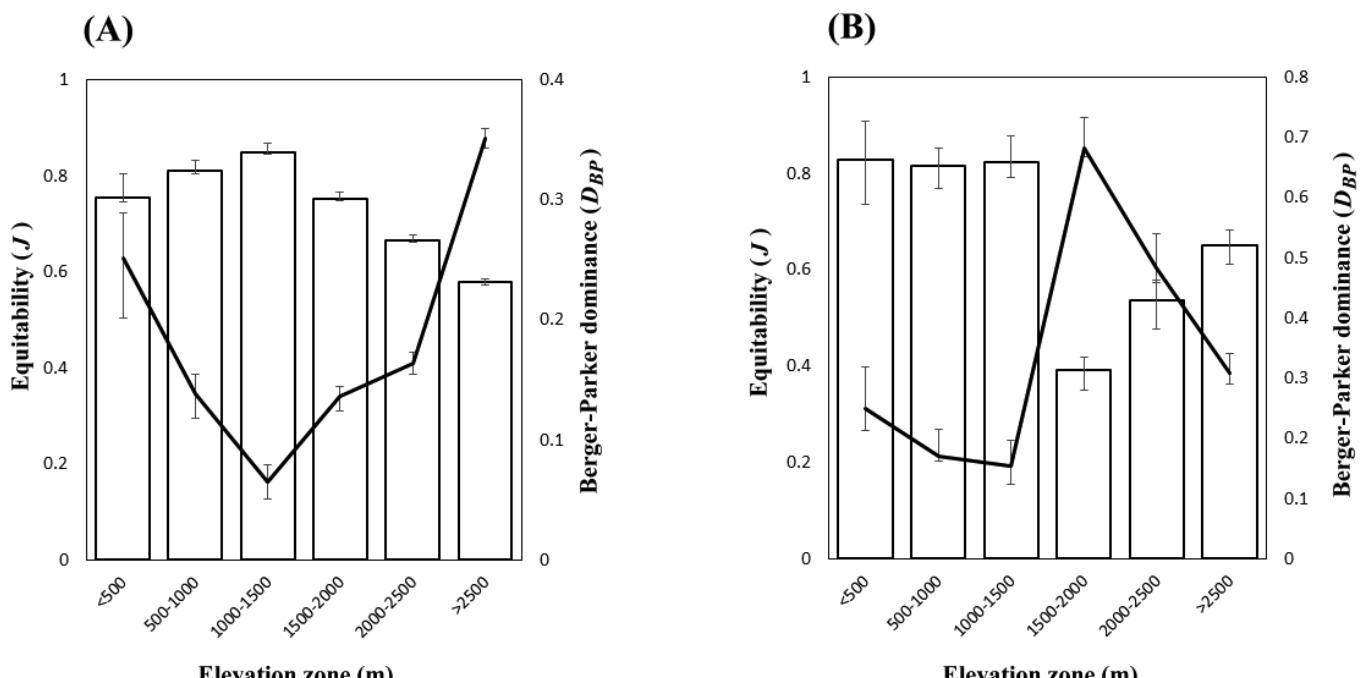


Fig. 6. Variation in Equitability (J) and Berger-Parker dominance (D_{BP}) of Diptera (A) and Auchenorrhyncha (B) during 12 months of sampling over six 500 m elevation zones at Doi Inthanon in 2014. Values of J (bars) and D_{BP} (lines) were computed in PAST and 95% confidence intervals obtained by bootstrapping using 9999 random samples. In Kruskal-Wallis H -tests there was a significant difference between the medians for Berger-Parker dominance in Diptera ($H = 26.7, p < 0.01$) and Auchenorrhyncha ($H = 14.9, p < 0.01$). Equitability was significantly different for Diptera ($H = 36.5, p < 0.01$) but not for Auchenorrhyncha ($H = 10.7, p = 0.0582$).

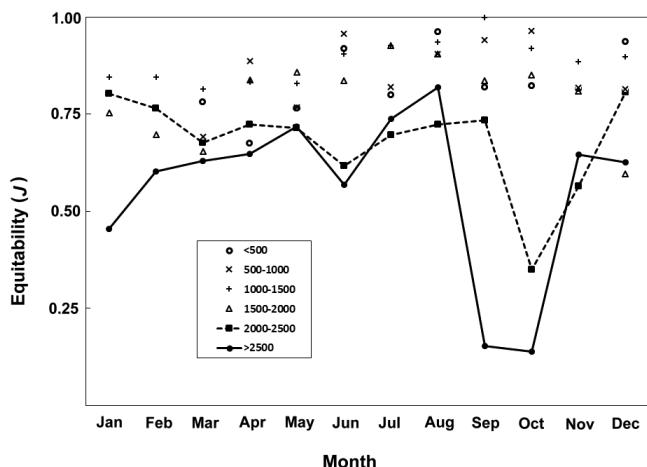


Fig. 7. Monthly variation in Equitability (J) of Diptera assemblages during 12 months of sampling over six 500 m elevation zones at Doi Inthanon in 2014. Only points linking data from elevation zones 2,000–2,500 m and $>2,500$ m are connected by lines. Equitability declines profoundly at higher elevations between September and November indicating a decline in evenness of Diptera assemblages with corresponding prevalence of a number of relatively abundant species compared with other times of year and other elevations.

Diptera (Fig. 8A) and Auchenorrhyncha (Fig. 8B) decays with elevational and temporal distance from the main peaks of α -diversity. Furthermore, for both orders, elevation has a ‘stronger’ effect than does time suggesting the importance of elevational zoning in determining assemblage composition. A better illustration of how turnover varies locally between adjacent elevations and months is provided by Mean Local Turnover (β_{WL}) of Diptera (Fig. 9A) and Auchenorrhyncha (Fig. 9B) where turnover is observed to be lower at higher elevations in all months except the pre-monsoon period in January and February. Additional support for assemblage composition of both orders being more temporally stable at higher elevations is provided by β_{WM} which reports how turnover varies between adjacent months within an elevation zone and which decreased with altitude (Fig. 10A, B). In general, β_{WL} of Diptera is higher in the latter half of the year at lower elevations (Fig. 9A) whereas for Auchenorrhyncha, β_{WL} appears to be highest during the dry cold and dry hot seasons between November and February.

Seasonality. The five seasonality measures were all positively correlated with elevation; for Diptera SM , $SM_{>6}$ and L_e were significantly and tightly correlated with elevation, SL and $SL_{>6}$ less so (Table 2). For Auchenorrhyncha $SM_{>6}$ and L_e were strongly correlated with elevation, SM , SL and $SL_{>6}$ less so (Table 3). Positive correlations between SM and SL were strong for both orders, weaker between SM and L_e , and weaker still between SL and L_e (Tables 1, 2). Each seasonality parameter provides slightly different information. L_e for example only characterises variance and does not utilise information on temporal sequences, as is the case in SL , thus increased values of L_e merely reflect greater evenness. However, we can conclude that at higher elevations (a) more species are active for a greater proportion of the year, (b) seasonal occurrence spans are longer and species with longer emergence spans are more frequent, and (c) the distribution of monthly occurrences is more even

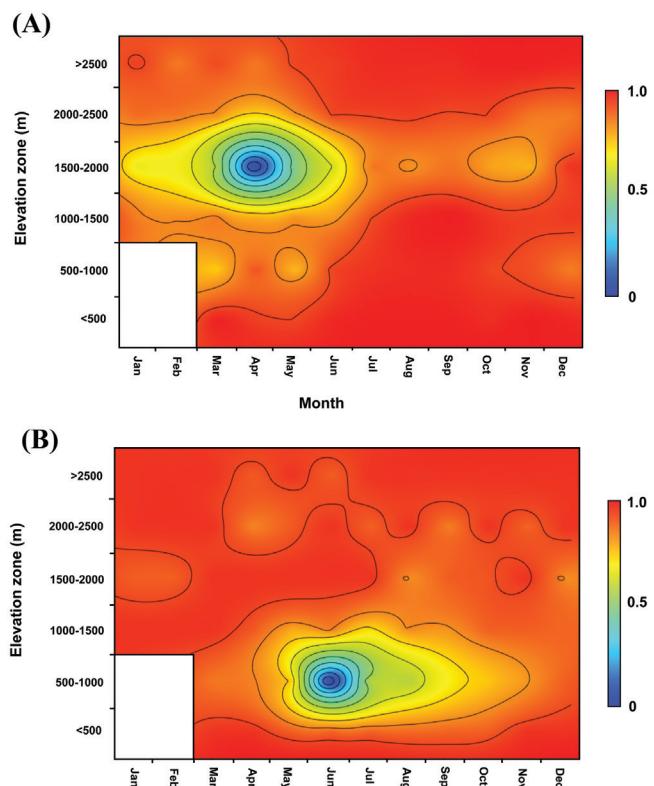


Fig. 8. Variation in species turnover measured as β_w of Diptera (a) and Auchenorrhyncha (b) during 12 months of sampling over six 500 m elevation zones at Doi Inthanon in 2014. Pairwise calculations of β_w between each quadrat of a grid of elevation and month with the quadrat with maximum species richness (April/1,500–2,000 m quadrat for Diptera and June/500–1,000 m quadrat for Auchenorrhyncha) were mapped using the multiquadric gridding algorithm in the gridding module of PAST. Values of β_w (indicated by colour scale bar) vary between 0 (complete identity) and 1.0 (complete non-identity). Data are not available for January and February at <500 m and 500–1,000 m.

than at low elevation. Clearly, the season in which adult Diptera and Auchenorrhyncha are active is prolonged at higher elevations. None of the seasonality parameters deal effectively with bivoltine or multivoltine phenologies. Below 1,500 m bivoltism or multivoltism occurred in 2.2% of 319 dipteran taxa and 4.2% of 108 Auchenorrhyncha whereas above 1,500 m the corresponding figures were 7.7% ($n = 349$) and 6.8% ($n = 73$).

DISCUSSION

Diptera and Auchenorrhyncha occurred as rich assemblages but with different spatiotemporal distributions of species diversity and abundance. Auchenorrhyncha were most species rich at lower elevations (500–1,500 m) in highly seasonal predominantly deciduous forest whereas Diptera favoured evergreen forests at 1,500–2,500 m. Elevational profiles of abundance were not coincident with species richness as in both orders abundance maxima occurred at higher elevations than did peak species richness. Assemblage composition was generally more even at elevations with maximum richness while the less diverse assemblages at higher elevations were dominated by a few very abundant taxa. Species richness and abundance of Diptera and Auchenorrhyncha were greatest

Table 2. Correlation of seasonality parameters for Diptera, SM , SL , $SM_{>6}$, $SL_{>6}$ and L_e with elevation during 12 months of sampling over six 500 m elevation zones at Doi Inthanon in 2014. Mean values of each parameter for each elevation zone were fitted to linear or binomial regression models in PAST. The equation used and values of r^2 and p are indicated. Correlations between parameters are indicated in the footnote.

Parameter	r^2	p	Equation
SM	0.928	0.002	$y = 0.236x + 1.509$
SL	0.804	0.016	$y = 0.208x + 2.261$
$SM_{>6}$	0.980	0.003	$y = 0.456x^2 - 0.823x + 1.797$
$SL_{>6}$	0.712	0.153	$y = 0.504x^2 - 1.553x + 12.076$
L_e	0.737	0.029	$y = 0.330x + 2.488$

(a) SM & SL are positively correlated ($r^2 = 0.9089$, $p = 0.0032$); (b) SM & L_e are positively correlated ($r^2 = 0.6013$, $p = 0.0699$); (c) SL & L_e are weakly positively correlated ($r^2 = 0.5002$, $p = 0.1160$).

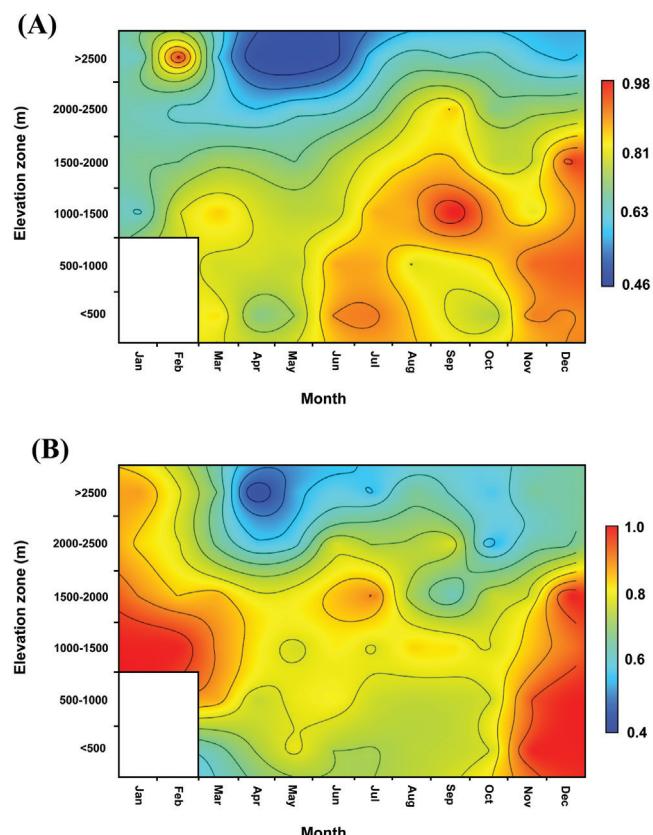


Fig. 9. Spatiotemporal variation in species turnover measured as Mean Local Turnover β_{wL} of Diptera (A) and Auchenorrhyncha (B) trapped during 12 months of sampling over six 500 m elevation zones at Doi Inthanon in 2014. Data were plotted on a grid of elevation zone (vertical axis) and months (horizontal axis) and mapped using the multiquadric gridding algorithm in the gridding module of PAST. Values of β_{wL} (indicated by colour scale bar) vary between 0 (complete identity) and 1.0 (complete non-identity). Data are not available for January and February at <500 m and 500–1,000 m.

around the time of the rainy season, in northern Thailand associated with the southwest monsoon between May and October. However, phenological profiles of species diversity and abundance of the two orders were not closely coincident as richness of Diptera peaked (81% of total richness and 60% of abundance) from March to June during the period immediately prior to the onset of the monsoon and during its early phase, while that of Auchenorrhyncha (71.4% of

total richness and 30% of abundance) occurred between May and August, extending more fully across the main monsoon period. Secondary peaks of abundance and richness occurred later in the year during September to November at the end of the monsoon period extending into the cold dry season that follows. For Auchenorrhyncha, this late monsoon peak accounted for 42% of total diversity and 38% of abundance and for Diptera, 37% of diversity and 21% of abundance.

It is clear that despite differing taxonomic positions, trophic functionality, habitat preferences and elevational profiles, richness and abundance of both Diptera and Auchenorrhyncha coincides with the timing of monsoon rains, as has been frequently observed in other insect taxa in tropical seasonal forests (Frith & Frith, 1990; Wiwatwitaya & Takeda, 2005; Plant et al., 2011). We do not imply that this correlation demonstrates that precipitation is causative (the monsoon rains also coincide with higher temperatures and decreased diurnal temperature range for example, both of which could be invoked as triggers of adult activity) but much as water plays a dominant role in the regulation of vegetation structure and dynamics of tropical seasonal forests, it may be a significant determinant of insect seasonality. The need for moist edaphic conditions for larval development of most of the dipteran taxa sampled here suggests that rainfall might have a strong influence on activity. Similarly, the correlation of flowering with monsoon rains might favour coincident activity of nectar-feeding Diptera, and early monsoon leaf flushing with associated increased vascular activity could promote activity of sap-feeding Auchenorrhyncha. Water availability probably promotes insect abundance primarily by influencing the availability of food resources but the exact mechanisms responsible are likely to be variable across different functional and taxonomic groups.

Bimodal abundance maxima associated with early- and late-monsoon precipitation in seasonal tropical forests have been reported elsewhere (Grootaert, 2009) but it is far from clear what causes bimodality. Regional differences across Thailand of abundance maxima of the dipteran families Empididae and Hybotidae were reported by Plant et al. (2011); for example, in northern Thailand the late-monsoon maximum was smaller than that in the early-monsoon (as reported here for a wider range of Diptera families) but in western

Table 3. Correlation of seasonality parameters for Auchenorrhyncha, SM , SL , $SM_{>6}$, $SL_{>6}$ and L_e with elevation during 12 months of sampling over six 500 m elevation zones at Doi Inthanon in 2014. Mean values of each parameter for each elevation zone were fitted to linear regression models in PAST. The equation used and values of r^2 and p are indicated. Correlations between parameters are indicated in the footnote.

Parameter	r^2	p	Equation
SM	0.526	0.103	$y = 0.171x + 1.607$
SL	0.471	0.131	$y = 0.268x + 1.974$
$SM_{>6}$	0.831	0.012	$y = 2.540x - 4.038$
$SL_{>6}$	0.651	0.052	$y = 4.845x - 1.457$
L_e	0.701	0.038	$y = 0.329x + 1.249$

(a) SM & SL are positively correlated ($r^2 = 0.9671$, $p = 0.0004$); (b) SM & L_e are weakly positively correlated ($r^2 = 0.5159$, $p = 0.1079$); (c) SL & L_e are very weakly positively correlated ($r^2 = 0.4248$, $p = 0.1607$).

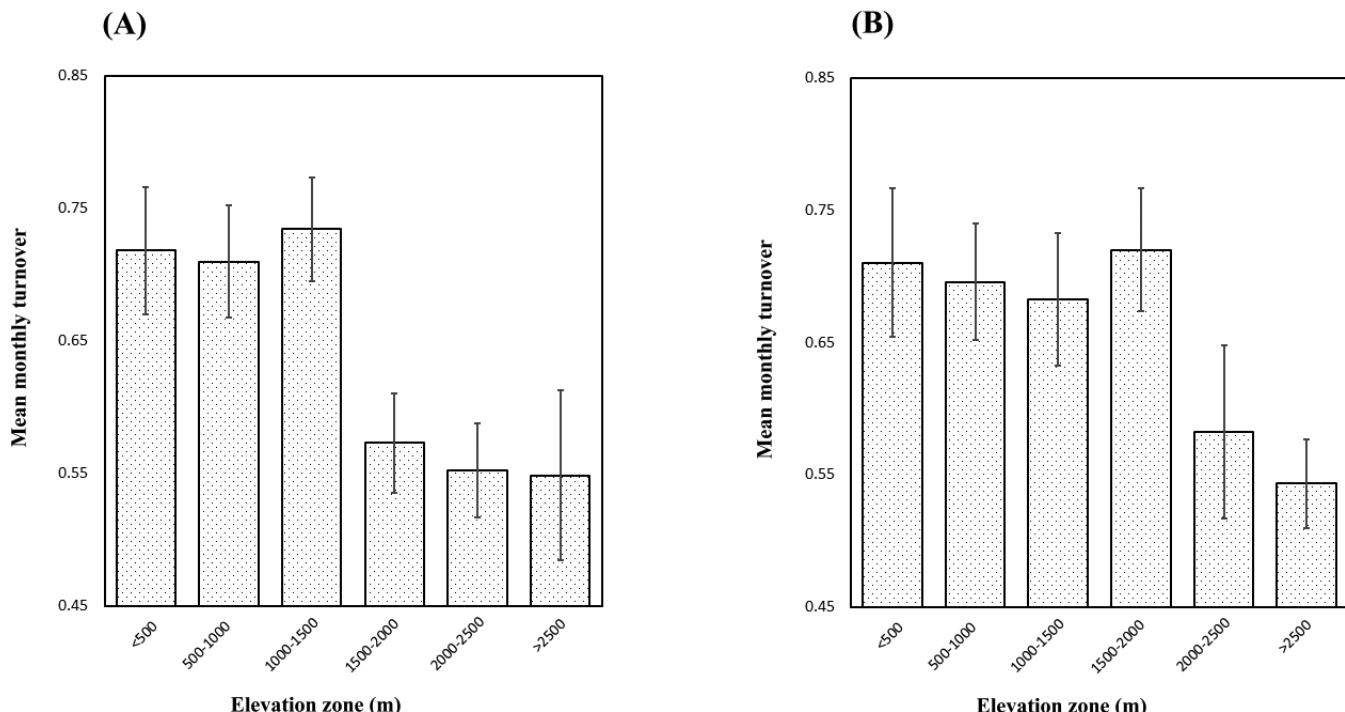


Fig. 10. Variation in Mean Monthly Turnover (β wM) of Diptera (A) and Auchenorrhyncha (B) during 12 months of sampling over six 500 m elevation zones at Doi Inthanon in 2014. The mean value of β wM in each elevation zone \pm standard error is indicated. Note that the vertical axis does not extend to zero. In Kruskal-Wallis H -tests there was a significant difference between the medians for Diptera ($H = 29.0$, $p < 0.01$) and Auchenorrhyncha ($H = 22.1$, $p < 0.01$).

Thailand, the relative magnitude of the early and late peaks was reversed and subtle differences in wet season correlation with abundance across different regions of Thailand were also noted. Diversity of Diptera at the two seasonal maxima on Doi Inthanon was structurally different as the assemblages comprising the early-monsoon peak were not only more speciose, but had greater evenness and lower dominance than those of the late-monsoon peak. There appears to be a general pattern in which more speciose assemblages had greater evenness than less diverse ones and that since species richness had an 'optimal' elevation, assemblages at more extreme (suboptimal) elevations had lower evenness and high dominance due to a small number of numerically abundant species.

Assemblage similarity of Diptera and Auchenorrhyncha decayed with elevational and temporal distance from the

main peaks of α -diversity. Local species turnover between adjacent elevation zones and months measured as β wM and β wL was lower at higher elevations (except during the pre-monsoon period which corresponded with the time when species-poor communities were rapidly transforming into species-rich ones coincident with the onset of the monsoon rains). Low β -diversity along spatially and temporally defined environmental gradients might indicate low levels of environmental filtering, high dispersal ability or increased local coexistence of competitive species (Spasojevic et al., 2014; Chalmandrier et al., 2015) but whatever its cause, attests a temporal stability in community structure at higher elevations on Doi Inthanon. If longer and wetter conditions prevailing at higher elevations permit progressive uncoupling of adult phenology from the intense seasonality lower down, the increased persistence of the limited number of species occurring at high elevation would manifest as decreased

local levels of assemblage turnover. All five seasonality measures we employed were positively correlated with elevation indicating that the season in which adult Diptera and Auchenorrhyncha are active is prolonged at higher altitudes. There may also be a higher incidence of bivoltism or multivoltism at higher elevations. Seasonality constrains the reproductive period of adults and may limit larval development to restricted periods of the year by changing availability or nutritive value of food resources. Semelparous or at least univoltine reproduction appears to be a response to temporally restricted but fairly predictable constraints on resources (Fritz et al., 1989). Relaxation of seasonality, for example by a longer and wetter rainy season at higher elevations, would permit longer adult flight periods and might favour iteroparity and multivoltism by allowing a longer adult reproductive period. More sustained moist soil conditions would also allow a longer period for larval development, especially for the edaphic larvae of dipteran taxa studied here.

This work has confirmed the frequent observation that in tropical seasonal forests, adult insect activity is often associated with the timing of seasonal precipitation and that spatial (elevation) and temporal (intra-annual) patterns of α -diversity vary between taxa. We also report profound variation in how diversity is structured throughout a year and across elevations, with two separate orders of insects demonstrating complex spatiotemporal dynamics of species richness, evenness and dominance, length of adult activity period, assemblage stability and species turnover. We only investigated intra-annual patterns but recognise that inter-annual variations might superimpose unseen and subtle influences (Valtonen et al., 2013). Improved appreciation of spatiotemporal patterns of diversity will be needed if we are to understand the ecological processes that sustain insect communities in tropical seasonal forests and assess their ability to phenologically track climatic conditions in response to climate change.

If diversity in tropical seasonal forests is not uniformly distributed in time and space, any attempt to assess global diversity by extrapolation and scaling up of local and regional diversity estimates requires that seasonal patterns be recognised. This is particularly important as tropical forests are exceptionally rich reservoirs of biodiversity and approximately 75% of their area experiences strong seasonality (Barlow & Woiwod, 1989). Our year-long sampling regime across all elevations probably recorded 80–90 % of total diversity of the selected focus taxa based on the Chao-1 estimator. The resources needed to achieve such detailed coverage are seldom available and most attempts to measure diversity in tropical seasonal biotopes are more spatially and temporally constrained, inevitably resulting in seasonal and spatial bias in the detectable species richness. For example, a three-month long sampling campaign across all elevations, during the early-monsoon diversity peak in April to June would have found only 381 species of Diptera compared with 531 from a full years' sampling. A similar three-month campaign during September to November would have been less productive yielding just 197; the two periods

would have only had 142 species in common with 239 and 55 species unique to the first and second periods respectively. If sampling had been restricted to an incomplete elevation range, observed richness would have been even lower; for different taxa have different diversity maxima and these in turn are sensitive to seasonality.

Although strong climatic seasonality has profound influences on the spatiotemporal dynamics of tropical insect communities, it remains a largely neglected variable. In particular, we note that local diversity will likely be underestimated from sampling regimes with unrepresentatively narrow temporal or spatial biases. Accurate estimation of local diversity underscores efforts to assess global diversity by scaling up from smaller areas. However, meaningful extrapolation is unlikely to be accomplished without understanding of the spatiotemporal dynamics of insect communities inhabiting seasonal forests and of the sampling restraints imposed by seasonality. An appreciation of the scale of seasonal uniqueness and temporal stability of communities is required. Understanding the seasonality of insect populations in tropical seasonal forests is particularly important as strong climatic seasonality is a geographically predominant characteristic of most tropical forests.

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