

Ghost species and optimal diversity: shared patterns between two tropical mountains within Auchenorrhyncha (Insecta: Hemiptera)

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Abstract. Altitudinal studies are usually carried out during a specific period of the year, which is supposed to be representative of the targeted insect diversity. Intra-annual variability is seldom investigated within tropical gradients, when it might influence diversity patterns. Two altitudinal gradients were compared here in tropical forests on two mountains, Mount Wilhelm (Papua New Guinea, 200–3,700 m.a.s.l) and Doi Inthanon (Thailand, 400–2,556 m.a.s.l), during the corresponding early wet-season sampling periods, to test a general spatial pattern of species diversity within tropical Auchenorrhyncha assemblages. We investigate the impact of selecting a seasonally optimal sampling period on determination of overall species diversity patterns. Shannon and Simpson diversity indices decreased as elevation increased on both gradients, as did species richness and abundance on Mount Wilhelm. Cluster analysis revealed numerous differences in altitudinal composition of dominant families between gradients. Our results revealed (1) the optimal sampling period with distinct seasonal variability in the diversity of assemblages, (2) that sampling only at an optimal period, had consequences on the number and the kind of species and families collected, but not on the diversity pattern, and (3) that the decrease of diversity indices with increasing elevation for the Auchenorrhyncha is not restricted to a local tropical gradient.

Key words. Auchenorrhyncha, elevational patterns, insect diversity, seasonality, tropical forests

INTRODUCTION

The study of altitudinal gradients raises important issues in ecology. Distribution of faunae and vegetation along mountain slopes are non-random (Gaston, 2003) and biotic transitions along gradients have attracted interest in comparative biology (Lomolino, 2001). Altitude is seen as a broad proxy for environmental and biological changes along mountain slopes, when elevation is the mere physical distance variable (Körner, 2007; McVicar & Körner, 2013).

Contemporary interest in altitudinal gradients has arisen for several reasons. First of all, the links between biotic gradients, areas of endemism, and biodiversity hotspots are important and useful in conservation biology (Burgess et al., 2007). Altitudinal gradients also offer numerous potential worldwide replicates (Sanders & Rahbek, 2012), allowing comprehensive meta-analysis and development of complex mathematical models, which are considerably increasing

our knowledge of this ancient biological problem (Gross & Snyder-Beattie, 2016). Finally, mountain slopes constitute an interesting field of research in the context of global climatic and environmental change (Brooker et al., 2007).

Elevational studies have been extensively carried out during the last decades (Guo et al., 2013; Beck et al., 2017). Still, Southeast Asia and Papua New Guinea are underrepresented (Muenchow et al., 2017). More than this geographical bias, the temporal component is still an important gap within current studies (Korhonen et al., 2010; Jones et al., 2012). A major time-component within insects is seasonality (intra-annual variation). Insects are strongly sensitive to temperature and rainfall variation, much more than vertebrates for example, and these are well-known to change drastically in the tropics. Because only a short temporal-window exists for events such as metamorphosis and adult emergence, and as most insects have short life duration, they exhibit strong intra-annual variation, in terms of species richness and evenness (Wolda, 1988). When seasonal variation is disregarded, differential emergences are ignored. The risk of misinterpretation may be even higher as climatic parameters also change with elevation, providing different pictures of the pattern (Beck et al., 2010; Lefebvre et al., 2018; Plant et al., 2018). Indeed, except in a few studies (Novotny & Basset, 1998; Grootaert & Kiatsoonthorn, 2003; Choochote et al., 2005; Belen & Alten, 2011; Srisuka et al., 2015; Plant et al., 2018), the temporal dimension in sampling protocols often has to be neglected. Most studies focus on a single optimal period, i.e., one in which more taxa and/or individuals are found than any other period. We will call the species

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that do not occur during an optimal period ghost species. Evidently, one might argue that they do occur, but not in a form available for sampling, either in a different stage of their life cycle or in a cryptic habitat. But the question remains, how biased are such truncated measurements when sampling is limited to an optimal period?

To quantify the biodiversity of these communities, numerous diversity indices are available in the literature. Data mining in order to find the most significant results should be avoided according to Morris et al. (2014). Here, in order to explore species richness and abundance, we used two consensually accepted diversity indices: Shannon and Simpson diversity indices (Smith & Wilson, 1996), which are useful for comparisons with other studies. These indices present complementary biases regarding rare/common species (Oksanen et al., 2016).

Insect groups that depend on disparate vegetation and climatic variation are key models to study such biological turnovers (Kemp et al., 2017). Here, our studied taxon is the Auchenorrhyncha suborder (Insecta, Hemiptera), comprising more than 19 families in this regional context. They are strictly phytophagous, sap-feeders or fungivores (Attié et al., 2008), strongly associated with their host-plant(s) (Wilson et al., 1994; Soulier-Perkins et al., 2007). Due to their feeding habits, the Auchenorrhyncha are expected to follow the pronounced spatial partition of the vegetation in tropical mountain forests (Le Cesne et al., 2015). Hence, Auchenorrhyncha appear to be a very interesting model for our elevational gradients comparison in the tropics.

Here, the comparison of two tropical mountains allows us to evaluate the level of generality of our findings, and highlight results not restricted to a single local gradient. The aim of this work is to test the following hypotheses: (1) within temporal bands that are seasonally comparable, both mountains (Mount Wilhelm, Papua New Guinea, and Doi Inthanon, Thailand) exhibit the same species diversity pattern, and (2) an optimal period gives the same quantitative and qualitative picture of insect diversity than a wider period. This last test is only possible because of the exceptional collecting effort at Doi Inthanon which was sampled throughout a whole year.

MATERIAL AND METHODS

Study sites. Doi Inthanon (DI) is Thailand's highest peak (18°35'N, 98°29'E, 2,565 m), located in Thanon Thongchai Range in the north-west of the country (80 km south of Chiang Mai). This peak is one of the last of the south-east Himalayan Arc. The vegetation structure is well-delineated (Plant et al., 2018). The lower gentler slopes are characterised by Dry Dipterocarp and Dry Evergreen forests, the average temperature is 27°C, and rainfall is less than 1,200 mm/year, mostly falling between May and October. At around 1,000–1,300 m, Mixed Deciduous and localised areas of *Pinus* become evident with Hill Evergreen influences increasing with elevation and becoming dominant between 1,300 m and 2,000 m. Above 2,000 m Moist Hill Evergreen forest

prevails and there is a small area of *Sphagnum* bog with surrounding *Rhododendron* scrub at the summit. The upper slopes have an average temperature of ca. 13°C and rainfall is more than 3,000 mm/year (Bedos, 1994; Khamyong et al., 2004; Plant et al., 2011); although rainfall is maximal between May and October it also occurs at other times and there is no pronounced arid season.

Mount Wilhelm (MW) is in Papua New Guinea. Our transect followed the crests of the north-east slope of the mountain, starting at 200 m.a.s.l. and extending to the upper tree limit at 3,700 m. The zonation of vegetation along the mountain slope corresponds to changes in temperature and humidity (Hope, 1976). At altitudes less than 1,000 m, the tropical rainforest is dominated by Dipterocarpaceae, the average daily temperature fluctuates between 25 and 30°C, and rainfall is greater than 4,000 mm/year. Between 1,000 m and 2,500 m, Lauraceae and Fagaceae are dominant and from 2,500 m to 3,000 m, Podocarpaceae become increasingly abundant; above 3,000 m, the sub-alpine vegetation is dominated by tree ferns (Cyatheaceae), the average daily temperature is ca. 8°C, and rainfall is less than 3,400 mm/year (Hope, 1976).

Protocols and study material. On MW, Malaise traps were positioned in eight altitudinal bands situated at 500 m intervals, from 200 m to 3,700 m (Appendix 1). On each altitudinal band, four Malaise traps were positioned, so a total of 32 traps were placed along this gradient.

On DI, a total of 12 Malaise traps were set along an altitudinal gradient on the eastern slopes of the mountain between 412 m and 2,545 m; traps were sited in seven locations (one to three traps per location) selected to represent major forest type transitions along the gradient (Appendix 1).

Environmental conditions on both mountains are, at first sight, very similar but vegetation zonation is different at the two localities: monsoon forests from DI versus equatorial ones from MW. DI and MW have not exactly the same climatic influences. However, they do share a short dry season and a long wet season (Novotny & Basset, 1998; Teejuntuk et al., 2002; Sukri et al., 2003; Plant, 2014). It seems that Auchenorrhyncha are sensitive to these intra-annual variations (Novotny, 1993). On DI, insects were trapped throughout the year, but for only 15 days (October/November) on MW, empirically inferred to be the optimal period for trapping Auchenorrhyncha. Because of such differences in protocol, we had to compare corresponding temporal bands of DI's diversity. The October/November period is the end of dry season and the beginning of wet season on MW (Novotny & Basset, 1998). Onset of the rainy season happens in April/May on DI (Teejuntuk et al., 2002).

The material comes from separate invertebrate sampling projects: Twin Peaks and Our Planet Reviewed Papua-New-Guinea 2012–2013. Twelve collecting points sampled during 8 weeks (24 trap-months) were available on DI whereas 32 collecting points sampled during 2 weeks (16 trap-months) were available on MW.

Table 1. Taxonomic results for all specimens collected in Papua New Guinea (Mount Wilhelm during October/November) and Thailand (Doi Inthanon, during April/May). For absolute comparison, these results must be weighted by the trap \times duration number (see text).

Taxa	Abundance		Number of species	
	Doi Inthanon	Mount Wilhelm	Doi Inthanon	Mount Wilhelm
Cicadomorpha	50	25	17	17
Aphrophoridae	28	1	4	1
Cercopidae	5	19	4	11
Cicadidae	0	3	0	3
Machaerotidae	2	0	1	0
Membracidae	15	2	8	2
Fulgoromorpha	657	442	51	168
Achilidae	32	72	5	19
Caliscelidae	2	0	2	0
Cixiidae	153	179	11	53
Delphacidae	304	24	8	18
Derbidae	6	116	4	63
Flatidae	3	6	2	5
Fulgoridae	0	1	0	1
Issidae	108	2	12	2
Lophopidae	3	0	1	0
Meenoplidae	36	41	2	6
Nogodinidae	5	0	1	0
Tropiduchidae	5	0	3	0
Ricaniidae	0	1	0	1
Total	707	467	68	185

Insects collected by Malaise trapping were preserved in 70% ethanol samples. In order to identify some specimens, the terminalia were dissected in KOH prior to examination. Morphospecies were established by the first author for Thailand samples and by the second author for those from Papua New Guinea, under the supervision of the last author. The morphological characters used were those generally used for the Auchenorrhyncha to describe new species and that could be well-illustrated in a key such as the one provided by Biedermann & Niedringhaus (2009) for Germany. The gigantic diversity of the family Cicadellidae (Cicadomorpha, Cicadelloidea) could not be sorted to morphospecies in the Thailand samples and therefore was not included in this work. Based on an earlier report, the collected cicadellids in Papua New Guinea had been sorted and represented 60% of the overall Auchenorrhyncha species richness and 84% of the overall Auchenorrhyncha abundance (numbers available in Le Cesne et al., 2015). In Thailand samples, we estimated a similar contribution of cicadellids.

Data analysis. To study alpha-diversity, abundance, species richness, Shannon, and Simpson diversity indices were analysed with the diversity function from {vegan} package (Oksanen et al., 2016), and polynomial (i.e., non-linear) regressions were based on square root-transformed values. The Simpson index of diversity (1-D) is hereafter referred to as Simpson index. Those indices were chosen because of their complementary biases and very common use, when both richness and abundance are taken into account.

Rarefied richness was not calculated because of the data composition (imbalanced species commonness). To study the beta-diversity of elevational assemblages, we calculated the Jaccard's dissimilarity index, an asymmetrical binary coefficient (Legendre & Legendre, 1998) that measures similarity between sites in terms of shared species. The index, obtained via the `vegdist` function from {vegan} package, considers a double absence as non-informative and tends to exaggerate dissimilarities; we used the abundance version for the same reasons as above. A nearest neighbour-joining algorithm was run on the distance matrix using the `nj` function from {ape} package (Paradis et al., 2004). Dominant families, in terms of abundance, were mapped on the resulting tree in order to interpret the clusters (i.e., the groups of more similar sites). All regressions and cluster analyses were run with R version 3.1.1.

Finally, for Thailand, we calculated the number of absent (relative to the whole year sampling) species (S), individuals (I), and families (F) for each month of the year. Chao1 bias-corrected and ACE estimates were also calculated with their standard errors using the `estimateR` function from {vegan} package.

RESULTS

Diversity and altitudinal patterns. For the studied period (April/May in Thailand; October/November in Papua

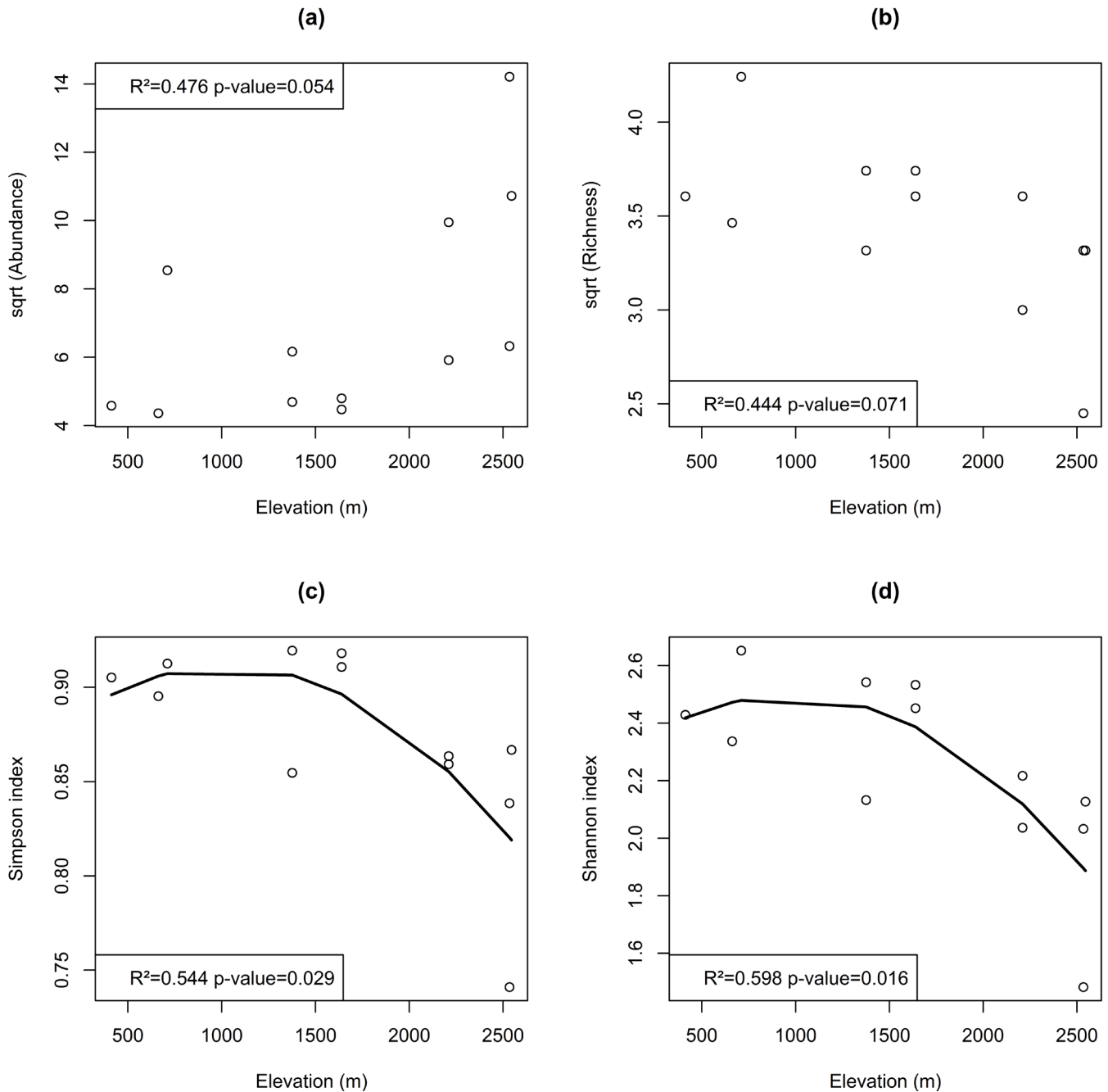


Fig. 1. Regressions between altitude and Abundance (a), Richness (b), Simpson (c), Shannon (d), on Doi Inthanon (Thailand) during the studied period (April/May). Lines are represented when regressions were significant ($p < 0.05$).

New Guinea), we identified 707 individuals of 68 species belonging to 15 families on DI, and 467 individuals of 185 species belonging to 13 families on MW. The taxonomic composition and abundance are presented in Table 1. The total relative abundance is about 7 individuals.trap⁻¹.week⁻¹ for both gradients, and the total relative richness is about less than 1 species.trap⁻¹.week⁻¹ for DI and about less than 3 species.trap⁻¹.week⁻¹ for MW. Similarly, the trap-weighted overall ratio of individuals/species is 0.11 for DI and 0.04 for MW. The DI selected samples (Table 1) represent 42.5% of the DI all-year species richness and 18% of the total abundance (not presented). It should be noted that in Table 1, although Derbidae were very species-rich (94 individuals for 19 species) in DI year-long samples, only six individuals for four species were found during the study period. This is

clearly an example of a family which does not have its peak diversity coinciding with the optimal period.

On DI there was no significant relationship between abundance or species richness and elevation ($p > 0.05$) (Fig. 1a, b). The results for Shannon and Simpson diversity indices ($p < 0.05$) revealed a “low-plateau” pattern (Fig. 1c, d). For the MW data, all regressions were statistically very significant with $p < 0.01$, and a monotonic diversity pattern was observed. For both gradients the species diversity distinctly decreased with altitude (Figs. 1, 2). Taking all the annual samples from DI into account, we observed a monotonic diversity pattern on DI identical to MW’s, without a low plateau (Fig. 3).

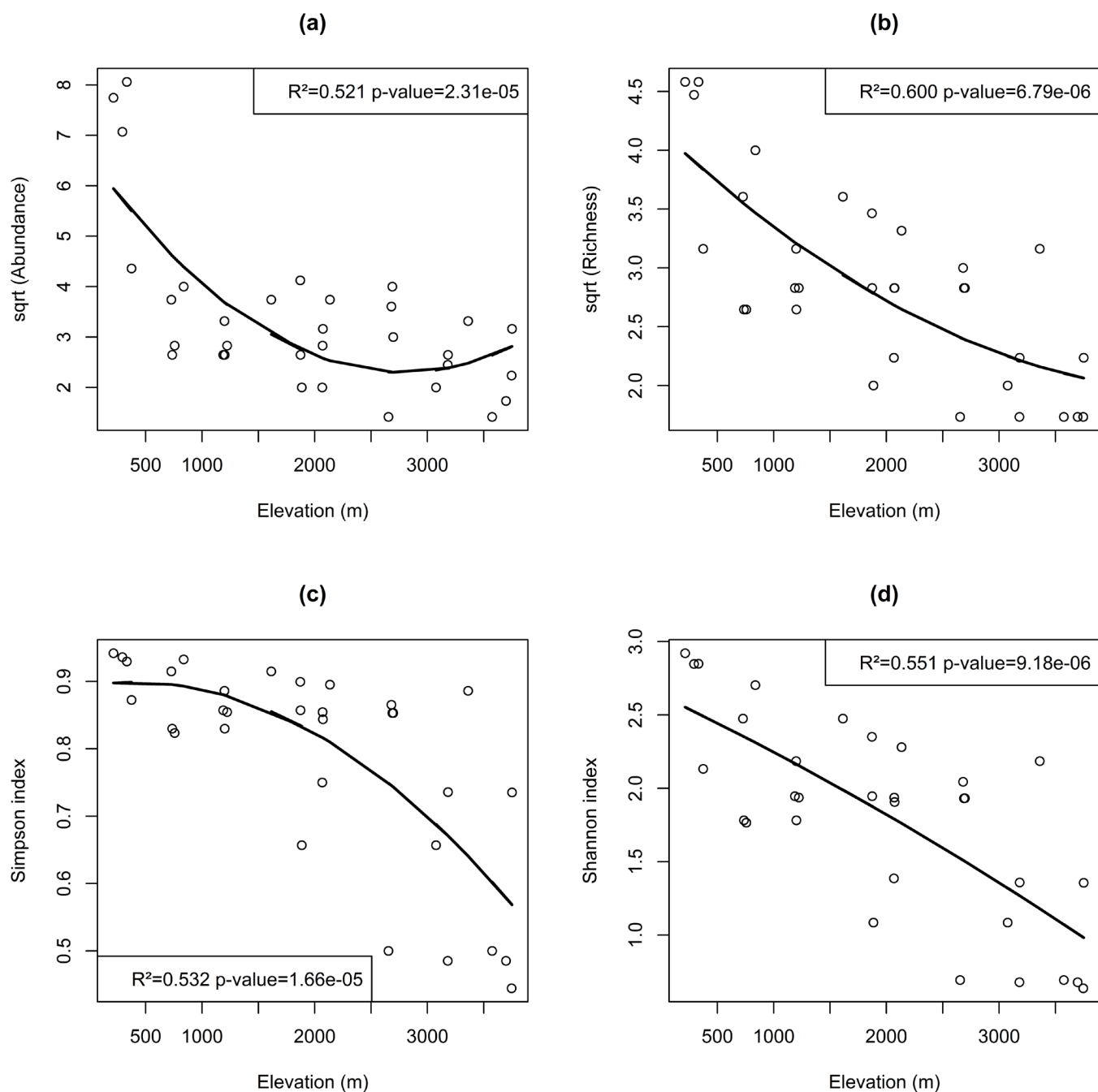


Fig. 2. Regressions between altitude and Abundance (a), Richness (b), Simpson (c), Shannon (d), on Mount Wilhelm (Papua New Guinea) in 2012. Lines are represented when regressions were significant ($p < 0.05$).

The biotic similarity (Fig. 4a, b) revealed by cluster analysis showed numerous differences in altitudinal composition between gradients. High (2,000–3,000 m) or mid (1,000–2,000 m) altitudes were never strictly clustered. Achilidae were most abundant and dominated in low altitude environments (412–710 m) on DI (Fig. 4a) but clearly occurred mostly around 2,000 m on MW (Fig. 4b). The Meenoplidae were more abundant at low altitudes on both mountains between 412–710 m (Fig. 4a) and 214–837 m (Fig. 4b). The Derbidae were not significant during the sampled period on DI (Fig. 4a, Table 1), but dominated various altitudinal clusters from low to high elevations on MW (Fig. 4b). The Delphacidae dominated various altitudes on DI (Fig. 4a), but only one elevation on MW (Fig. 4b). Delphacids on DI are mainly represented by two abundant species: the brown

planthopper, *Nilaparvata lugens* (Stål, 1854), and the white-backed planthopper, *Sogatella furcifera* (Horváth, 1899); both were present but not significant on MW. Cixiidae are dominant in numerous low- to mid- altitude environments, and always at the summit, on both mountains (Fig. 4a, b). With the whole year sampling on DI, links between dominant taxa and elevational clusters change (Fig. 5), Delphacidae dominance is more apparent whereas the Cixiidae's is less or disappears slightly.

Seasonality on Doi Inthanon. For Thailand's selected period (April/May, shaded in Table 2), 52% of the species biodiversity was absent (74 for a total of 142) and four families were missing out of the 19 identified, which represent 21% of the family diversity. However, 31% of

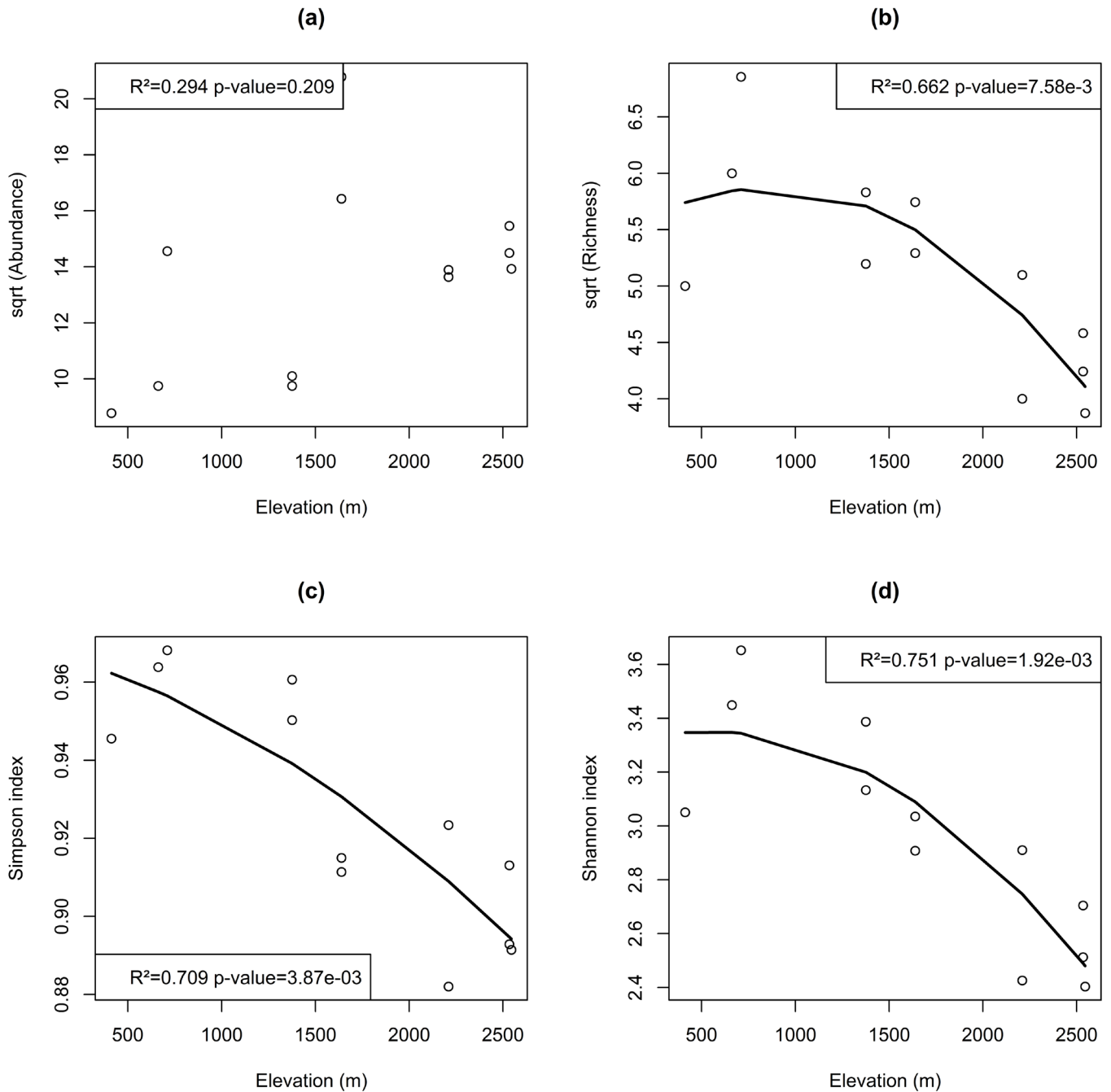


Fig. 3. Regressions between altitude and Abundance (a), Richness (b), Simpson (c), Shannon (d), on Doi Inthanon (Thailand) during the whole Twin Peaks project (2014). Lines are represented when regressions were significant ($p < 0.05$).

the project specimens were collected during that period. But more than this, the temporal species- and family- turnover is considerable (see Chao and ACE indices in Table 2). The number of absent species (S) and families (F), i.e., in ghost species distributions, both reach a local minimum around May (see also S1 index in Table 2). The mean number of months for species-occurrence was 2.76 (median = 2; mode = 1). Similarly, the mean number of months for family-occurrence was 6.53 (median = 6; mode = 11). As supplementary information, we noted that only four families occurred with a single-month duration, never at the same time and outside the optimal period (not presented).

DISCUSSION

Diversity patterns and seasonal scale. In this comparative study, locations, latitude, and longitude differ, as do their respective biogeographic realms. Furthermore, one is continental (Thailand), the other insular (Papua New Guinea). They both cover wide and similar elevational ranges between 200–3,700 m and 700–2,600 m, what Rahbek (2005) calls complete gradients. Several elevational patterns have been observed globally, compared and explained through various hypotheses (McCain & Grytnes, 2010; see also, for historical perspectives, Webb et al., 2002; Losos, 2008; Wiens et al., 2010). Though maximal diversity often occurs at mid-elevations and might be a general global pattern (Rahbek, 1995; McCain, 2004; Escobar et al., 2005), we corroborate

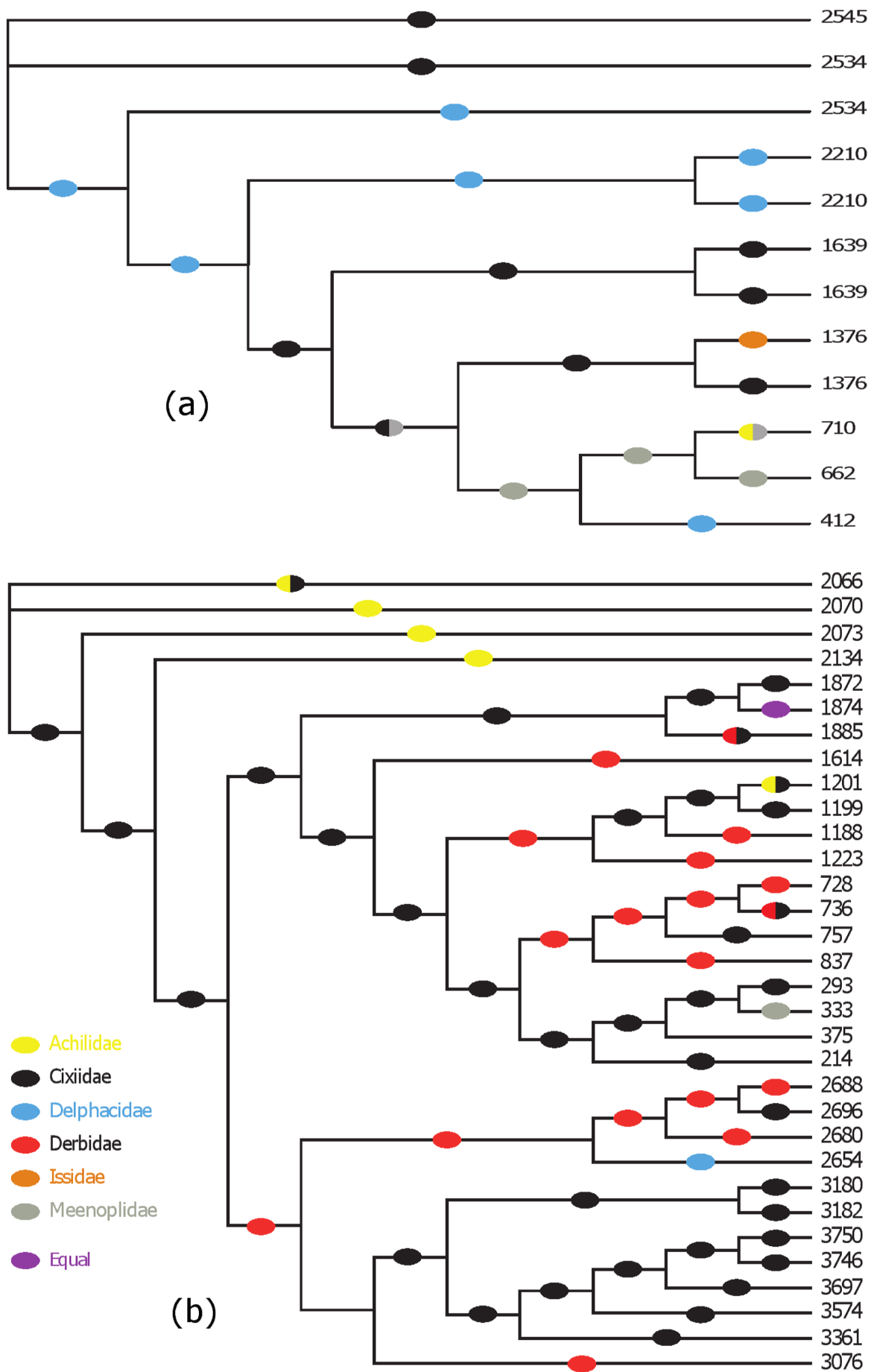


Fig. 4. Altitudinal clustering for Doi Inthanon (a) and Mount Wilhelm (b), using Neighbor Joining on Jaccard's dissimilarity index. Dominant families (in terms of abundances) are named on branches. Tips correspond to trap altitudes. On one specific branch (in (b)), "Equal" means that no families were particularly dominant.

Table 2. Number and proportion of absent families, species, and individuals for each month (1–12, i.e., January to December) compared to the whole year on Doi Inthanon in 2014. F = number of absent families; S = number of absent species; S1 = number of species found at only one month; I = number of absent individuals; % indicates the percentage of the total; Chao1 and ACE are provided with standard errors (\pm SE). There was a total of 19 families, 142 species, and 2,305 individuals. The extracted period is shaded.

Month	F	S	S1	I	%F	%S	%I	Chao1 (\pm SE)	ACE (\pm SE)
1	17	140	0	2,303	89.47	98.59	99.91	3 (2.041)	NA (NA)
2	12	130	2	2,279	63.16	91.55	98.87	19 (7.079)	22.81 (2.371)
3	7	101	8	2,125	36.84	71.13	92.19	64.33 (13.63)	78.13 (5.502)
4	6	101	5	1,849	31.58	71.13	80.22	69.50 (17.93)	72.90 (5.232)
5	5	85	11	2,054	26.32	59.86	89.11	115.1 (29.62)	116.2 (6.415)
6	6	90	9	2,092	31.58	63.38	90.76	106 (29.02)	93.03 (4.637)
7	8	108	4	2,196	42.11	76.06	95.27	91 (38.68)	65.04 (4.308)
8	8	113	4	2,201	42.11	79.58	95.49	42 (9.250)	53.40 (4.540)
9	8	101	6	2,071	42.11	71.13	89.85	91 (28.51)	91.82 (5.114)
10	8	111	4	1,701	42.11	78.17	73.80	65.20 (21.92)	73.46 (4.625)
11	10	120	1	2,265	52.63	84.51	98.26	48.25 (18.74)	62.10 (5.037)
12	9	112	4	2,219	47.37	78.87	96.27	55.50 (16.38)	66.74 (4.737)

the most common pattern already reported for this group (Le Cesne et al., 2015): a quasi-monotonic decrease in species diversity with elevation (Figs. 1, 2). Since the same diversity pattern is observed for DI and MW, it is likely that other tropical mountains will provide similar results. This suggests 1) that our comparison is consistent and 2) that environmental drivers should be investigated (spatially and seasonally). Diversity may be positively related to temperature or elevational area, or may be negatively related to precipitation (McCain & Grytnes, 2010). When the all-year samples are considered, the same decrease in diversity with elevation is observed in Thailand. This result means that additional sampling throughout the year does not change the species richness pattern observed during the optimal period. We cannot reject the possibility that the increase in abundance on DI could be caused by a sampling effect, even if parallel richness is high. When the total abundance and number of species on both mountains (Table 1) are weighted by the number of traps and months, the abundances between DI and MW are similar while the richness is greater on MW than on DI. Either it is due to chance alone, or the absolute richness is just higher on MW.

We identified different transitions between low, mid, and high altitudes, dominated by some Auchenorrhyncha families. At the family-level scale, altitudinal assemblages differ between these two tropical mountain forests (Fig. 4a, b). The delphacids' high abundance at many high elevation sites on DI (Fig. 4a) is unexpected. The two most abundant species (*N. lugens* and *S. furcifera*) are known to be major rice pests in Asia, their occurrence has already been registered in Thailand (Catindig et al., 2009; Bartlett et al., 2014). Many applied surveys state their nymphs are not supposed to survive below 20°C (Dyck et al., 1979; Asai

et al., 1985). Clearly, what we knew about their nymphs must be updated (Dyck et al., 1979; Asai et al., 1985; Tu et al., 2013). Therefore, we can wonder and/or might worry about their potential impact(s) on summit endemic species, as they are non-native super-competitors in similar contexts (Dyck et al., 1979). We hope to draw conservation biology and local management policies' attention on this marginal but quite concerning case.

Links between dominant taxa and vegetation can change due to several reasons such as the seasonal variation, or the feeding habits of the different generations and/or life stages (Gadelha et al., 2017), but a seasonal sampling effect is in each case, especially in the tropics, an important variable (Abernethy et al., 2018). In our case, as shown by Figs. 4a and 5, we observe a marked difference in the dominance depending on the seasonal scale we are looking at. Therefore, such biotic similarity is time-dependent. We could infer a seasonal replacement phenomenon between abundant taxa in each biotope along tropical mountain forests. Further investigations might yield extremely interesting issues for ecological surveys in tropical environments.

Optimal diversity and ghost species. In many altitudinal studies, the temporal dimension (i.e., seasonality) is not fully considered, and the results are based on an optimal period which depends on the elevational band sampled. This is of course a consequence of limited scientific resources and the great amount of time such sampling techniques require. However, even if an optimal period is intuitive with respect to insects' seasonality, it is sometimes inadequate to study their complete biodiversity. As we can see in Fig. 4, each altitudinal band (biotope) comprises many families, but dominant families do not occur in so many biotopes. That

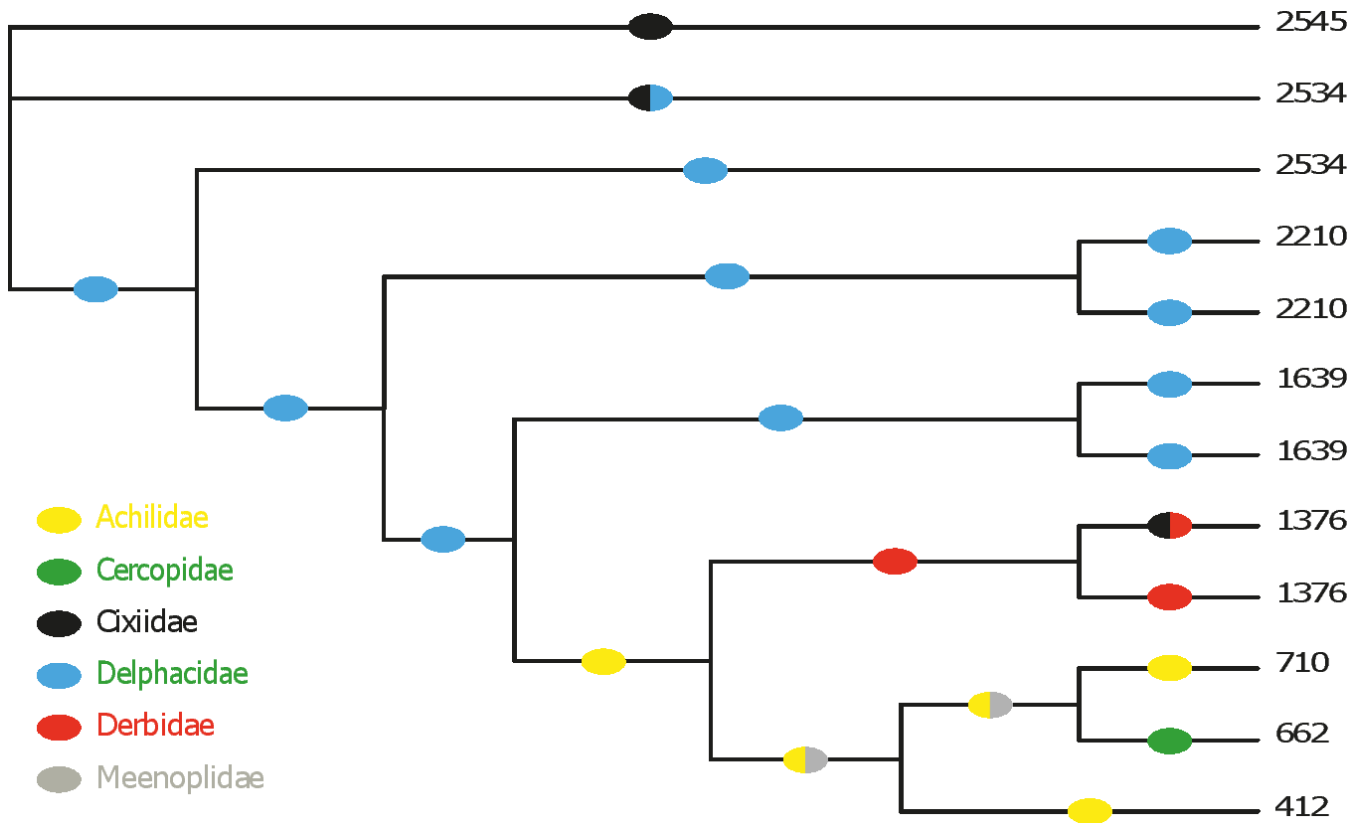


Fig. 5. Altitudinal clustering for Doi Inthanon's whole-year trapping, using Neighbor Joining on Jaccard's dissimilarity index. Dominant families (in terms of abundances) are named on branches. Tips correspond to trap elevations.

is also true of seasonal assemblages (Table 2), suggesting a strong spatiotemporal structure of insect diversity in the tropics (Plant et al., 2018).

Here we show there is indeed a period of optimum diversity for Auchenorrhyncha, which occurs around May on DI (Table 2) and in November on MW (as reported by Novotny & Basset, 1998). The optimal periods occur at different times of the year, corresponding in each case with the transition period at the beginning of the wet season, as shown in previous studies (Novotny, 1993). We can infer the transition season, from dry to wet, to be a broad potential cause of optimal species diversity. It coincides with the rising sap, probably influencing the overall Auchenorrhyncha diversity. Although, if it was the main factor, we would expect the peak in diversity to be reached in the greenest altitudes at the beginning of the wet season, which is not the case here (certainly not at low elevations). Clearly, sampling Doi Inthanon in May for Auchenorrhyncha would be the best compromise to catch maximum families and species. However, our results (Table 2) show that qualitatively, an optimum gives a poor picture of diversity: even at the best moment (in May), 60% of Auchenorrhyncha species and 26% of Auchenorrhyncha families are absent (Table 2). Whilst sampling during the optimum period appears to be representative of how the pattern of species richness changes with elevation, the information of how species richness varies away from the optimum is lacking. It feeds back the MW dataset: capturing a good qualitative picture necessitates other protocols than just October/November sampling. However,

an optimal period is quantitatively sufficient to identify diversity patterns.

Our results also suggest that changes in assemblages happen very quickly (1–2 months) at both species and family level. Consequently, it is difficult to predict how reliable the MW samples would be in predicting overall diversity. To date, it is unclear how Auchenorrhyncha communities would vary with altitude throughout the year on MW (Novotny & Basset, 1998). To answer this we need whole-year trapping studies, with data like those of DI. More comparative surveys will help the understanding of local altitudinal distributions in seasonal environments.

We highlight that seasonality is a major component of entomological diversity in tropical mountain forests. Nonetheless, we show that temporally truncated gradients (i.e., temporal-biased sampling) are sufficient for discovering the elevational pattern of diversity. We also point out: if assemblages of insect taxa like Auchenorrhyncha change through the year (and they change considerably), historical hypotheses, based on such protocols, are likely to give erroneous results (see also Beck et al., 2010). For instance, sister species could occur during opposite seasons, resulting in completely biased taxa-sampling, and therefore the potential evolutionary impacts of ecological speciation might go unnoticed. We refer to such taxa as ghost species (absent because they occur only in a suboptimal period). Ghost species are important for the understanding of tropical diversity patterns and should not be neglected.

The aim of this work was to investigate a concrete example of the consequences of an optimal sampling on tropical patterns of species diversity. As a next step, studying and integrating phenological information, in a phylogenetic context, should enable a better understanding of the origin and evolution of Auchenorrhyncha's diversity in tropical mountain forests. A better knowledge and understanding of communities' structure along elevational gradients would enhance predictive models for species responses to global changes (D'Amen et al., 2017). Finally, all insects were collected using the same method (Malaise trapping) but alternative sampling methods might yield further interesting perspectives on patterns of species diversity (Chao et al., 2005).

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APPENDIX

Appendix 1. Trap locality, altitude (m.a.s.l), GPS position, and year of sampling for both datasets.

Area	Altitude	Latitude/Longitude	Year
Doi Inthanon	412	18°29'57.0"N 98°40'06.2"E	2014
Doi Inthanon	662	18°32'27.6"N 98°36'00.5"E	2014
Doi Inthanon	710	18°32'20.5"N 98°36'05.3"E	2014
Doi Inthanon	1376	18.546°N 98.509°E	2014
Doi Inthanon	1376	18.546°N 98.509°E	2014
Doi Inthanon	1639	18.523°N 98.493°E	2014
Doi Inthanon	1639	18.523°N 98.493°E	2014
Doi Inthanon	2210	18.555°N 98.479°E	2014
Doi Inthanon	2210	18.555°N 98.479°E	2014
Doi Inthanon	2534	18.585°N 98.485°E	2014
Doi Inthanon	2534	18.585°N 98.485°E	2014
Doi Inthanon	2545	18.585°N 98.483°E	2014
Mount Wilhelm	293	5°44'23.63"S 145°19'47.07"E	2012
Mount Wilhelm	333	5°44'27.71"S 145°19'45.79"E	2012
Mount Wilhelm	375	5°44'41.24"S 145°19'37.77"E	2012
Mount Wilhelm	214	5°44'14.89"S 145°19'56.13"E	2012
Mount Wilhelm	728	5°43'55.06"S 145°15'7.79"E	2012
Mount Wilhelm	736	5°43'57.71"S 145°15'20.04"E	2012
Mount Wilhelm	757	5°43'57.05"S 145°15'24.54"E	2012
Mount Wilhelm	837	5°43'39.91"S 145°15'28.59"E	2012
Mount Wilhelm	1188	5°43'15.15"S 145°16'10.07"E	2012
Mount Wilhelm	1201	5°43'15.68"S 145°16'13.09"E	2012
Mount Wilhelm	1223	5°43'15.24"S 145°16'17.28"E	2012
Mount Wilhelm	1199	5°43'16.93"S 145°16'13.10"E	2012
Mount Wilhelm	1872	5°45'34.45"S 145°14'8.19"E	2012
Mount Wilhelm	1874	5°45'35.68"S 145°14'5.02"E	2012
Mount Wilhelm	1885	5°45'39.30"S 145°13'24.72"E	2012
Mount Wilhelm	1614	5°45'11.56"S 145°14'13.32"E	2012
Mount Wilhelm	2073	5°45'32.32"S 145°11'9.84"E	2012
Mount Wilhelm	2070	5°45'36.64"S 145°11'10.53"E	2012
Mount Wilhelm	2066	5°45'39.70"S 145°11'9.72"E	2012
Mount Wilhelm	2134	5°45'26.25"S 145°11'0.29"E	2012
Mount Wilhelm	2688	5°48'54.98"S 145°9'23.28"E	2012
Mount Wilhelm	2680	5°48'53.88"S 145°9'28.66"E	2012
Mount Wilhelm	2654	5°48'53.06"S 145°9'31.80"E	2012
Mount Wilhelm	2696	5°48'53.54"S 145°9'20.17"E	2012
Mount Wilhelm	3180	5°48'24.11"S 145°4'22.52"E	2012
Mount Wilhelm	3076	5°48'26.71"S 145°4'25.08"E	2012
Mount Wilhelm	3182	5°48'25.00"S 145°4'19.70"E	2012
Mount Wilhelm	3361	5°48'4.65"S 145°4'8.61"E	2012
Mount Wilhelm	3750	5°47'10.11"S 145°3'35.44"E	2012
Mount Wilhelm	3697	5°47'13.82"S 145°3'34.46"E	2012
Mount Wilhelm	3746	5°47'8.32"S 145°3'28.94"E	2012
Mount Wilhelm	3574	5°47'27.23"S 145°3'29.58"E	2012