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**Elevational filtering and the evolution of planthoppers (Hemiptera, Fulgoromorpha)
in Papua New Guinea**

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Abstract

Along elevational gradients, phylogenetic relatedness patterns constitute a considerable source of information, and may shed light on ecological processes that structure communities. This study focuses on community phylogenetic structure of planthoppers, specifically the species-rich and abundant Fulgoromorpha families (Hemiptera, Auchenorrhyncha), Cixiidae and Derbidae+Achilidae, along an elevational gradient on Mount Wilhelm (Papua New Guinea). In order to assess the factors driving planthoppers community composition, we recorded abundance data for planthoppers species at each elevation and we generated a molecular phylogeny of the local species, using Bayesian Inference. We analyzed 168 individuals representing 59 local morphospecies. Using a fully resolved and well-supported phylogeny, we then investigated the phylogenetic structure of the communities by performing a Spatial Analysis of Community Diversity. We show that Cixiidae are phylogenetically clustered along the elevational gradient, whereas Derbidae+Achilidae harbour a random structure, suggesting that local adaptation to elevation shapes community structure of Cixiidae, but not that of Derbidae+Achilidae. Our findings highlight the importance of phylogenies in the study of tropical elevational gradients.

Key words: Achilidae; Cixiidae; community diversity; Derbidae; elevational gradient; phylogenetic patterns; planthoppers; tropical rainforest

TROPICAL RAINFORESTS ARE GENERALLY RECOGNIZED AS BEING PART OF THE MOST BIODIVERSE TERRESTRIAL ECOSYSTEMS ON EARTH, but they are also among the most threatened by human land use. In order to maintain this tropical biodiversity, primary forests have to be kept in the best state possible since there is no substitute (Gibson et al. 2011). Those diverse ecosystems can be properly protected and managed only if the fauna and flora that compose them are better known and if the underlying evolutionary processes, such as local adaptation and ecological interactions, are documented and disentangled. As stated by Dioum in 1968 "In the end we will conserve only what we love, we will love only what we understand, and we will understand only what we are taught". However human activity and land use is not the only threat for biodiversity. Climatic changes drastically impact biodiversity and tropical communities appear to be more sensitive to temperature increases compared with temperate communities, especially in montane environments because of sharp environmental variations over short spatial scales (Sheldon et al. 2011). Elevational gradients therefore represent an appropriate system for evaluating the structure of species assemblages in a variable environment (see Graham et al. 2014), which in turn may shed light on community response to environmental changes.

Elevational gradients have been widely studied (Rahbek 1995, 2005; McCain & Grytnes 2010; Sanders et al. 2003; Mouquet et al., 2012; Manel et al. 2014; Lessard et al. 2016; Chatelain et al. 2018; Lefebvre et al. 2018), but incorporating phylogenetic information now allows to shed light on specific processes that shape the structure of communities along such gradients (Graham & Fine 2008; Graham et al. 2009; Pellissier et al. 2013; Chazot et al. 2014; Manel et al. 2014; Lessard et al. 2016). Indeed, over the last two decades, phylogenetic information has been increasingly incorporated into community ecology studies, either as a proxy for species' ecological traits (ecophylogenetics, Webb et al. 2002, Cavender-Bares et al. 2009), to correct for

non-independence of co-occurring species in the analyses of species' traits (e. g., Losos et al. 2003) or to detect particular patterns, such as phylogenetically non-random extinctions in communities driven by climate changes (Thuiller et al. 2011). Species assemblages may be mediated by random processes, such as dispersal, extinction and drift, and adaptive processes, such as local adaptation or interactions with other species, which are themselves mediated by traits. In practice, it is often difficult to know which traits are involved in such adaptive processes. Ecophylogenetics (Webb et al. 2002) attempts to circumvent those limitations. The rationale of ecophylogenetics is that, if traits are phylogenetically conserved, phylogenetic structure should reflect trait structure, and therefore should inform on underlying processes that shape community structure. If the main process acting on community structure is local adaptation, leading to environmental filtering (i. e., the fact that only species with specific adaptations can live in a given environment), co-occurring species are expected to share multiple traits involved in local adaptation, and therefore to be more closely related than non-co-occurring species. Such phylogenetic pattern is called phylogenetic clustering (Webb et al. 2002). Conversely, if local adaptation is not important (for instance, at a scale where there is little variation in environmental conditions) but competition between species is the main driver of community structure, resulting in mutual competitive exclusion among species that use the same resources, co-occurring species are expected to differ in many traits related to resource use, and therefore to be less closely related than non-co-occurring species. Such phylogenetic pattern is called phylogenetic overdispersion (Webb et al. 2002). Ecological processes can therefore be inferred from phylogenetic patterns. Caution must be taken, however, because in some cases, such as adaptive radiations across an environmental gradient, adaptive traits are not phylogenetically conserved, and community phylogenetic overdispersion reflects adaptive

radiation (and therefore adaptation to a range of environmental conditions) rather than competition. Here we use an ecophylogenetic approach to infer the main processes that shape Hemiptera Fulgoromorpha insect community structure along an elevational gradient in Papua New Guinea, on the Mount Wilhelm (4,509 meters high).

Papua New Guinea (PNG) is one of the countries with most preserved landscape, since three quarters of the land are covered by native forest. It is one of the less explored areas in the world, where biodiversity is suspected to be richest. In PNG, village communities own 97% of the land. As such, they are important decision makers in the preservation on their lands. In Wanang and Mount Wilhelm villages, ten clans have decided to be involved in conservation projects instead of logging. Fieldwork for the present study was done on their lands. This study, on Hemiptera Fulgoromorpha, is part of a large sampling effort to describe and analyze biodiversity patterns in multiple organisms in the mount Wilhelm (Leponce et al. 2016).

Hemiptera Fulgoromorpha is a diverse group of phytophagous insects that depends on plant species it feeds on. They have modified mouthparts allowing them to pierce and suck the sap of the plant for most of them. Fulgoromorpha do not undergo complete metamorphosis and as such the nymphs resemble the adults and generally have a similar diet. These insects feed and live on their hostplants. Some are polyphagous and have a large range of possible hostplants but many Fulgoromorpha depend on a few hostplants and can be highly specialized, thereby incurring a strong dependence to the biotope in which their hostplants can be found. As such, Fulgoromorpha species assemblages may vary with vegetation profile along environmental gradient. In addition, hostplant use can incur competition among species, which may also impact structure of species assemblages. Here we attempt to disentangle the impact of environmental filtering (due to local adaptation) and competition by applying ecophylogenetics to

Fulgoromorpha communities from the Mount Wilhelm. Specifically, 1) if the phylogenetic structure of communities is clustered (i. e., if co-occurring species are more closely related than expected at random), this may indicate environmental filtering, possibly driven by elevation and co-varying factors, such as vegetation; 2) if the phylogenetic structure of communities is overdispersed (i. e., if co-occurring species are less closely related than expected at random), this may indicate competitive exclusion; 3) if phylogenetic structure does not depart from neutral expectation, no conclusion can be drawn. Indeed, such neutral structure could stem from neutral processes, from competitive exclusion and environmental filtering cancelling out each other, or simply from a lack of statistical power.

MATERIAL AND METHODS

STUDY SITES.—Fieldwork was conducted along an elevational transect following the east slope of Mount Wilhelm in Papua New Guinea ($5^{\circ}44'14.89''\text{S}$, $145^{\circ}19'56.13''\text{E}$ to $5^{\circ}47'27.23''\text{S}$, $145^{\circ}3'29.58''\text{E}$). The elevational range extends from 200 to 3700 m, which represents the limit of the forest. The vegetation zonation along the mountain slope shows successive flora profiles and corresponds to changes in humidity and temperature. As described in Leponce *et al.* (2016), the temperature decreased linearly, dropping 5.4°C per 1000 m of increase in elevation, so the mean temperature ranged between 27.4°C at 200 m and 8.6°C at 3700 m during the collecting period. Under 1000 m, the rainfall is generally greater than 4000 mm/year and a mixed lowland forest is observed where the Dipterocarpaceae are found (Appanah 1998) along with Fagaceae, Nothofagaceae, Lauraceae, Cunoniaceae, Myristicaceae (Leponce et al. 2016). Between 1000 and 2500 m, the Lauraceae and Fagaceae tend to dominate. Then the Podocarpaceae become increasingly abundant from 2500 to 3000 m. Finally, above 3000 m, the rainfall is less than 3400

mm/year and then the Cyatheaceae dominate with a few emerging Podocarpaceae and shrubs, then appears a grassland above the tree line, around 3800 m.

INSECT SURVEY.—Insects were collected by malaise traps between October, 16th and November, 1st 2012 for the elevations 2200 m up to 3700 m, and between October, 25th and November, 10th, 2012 for the elevations 200 m up to 1700 m (Leponce et al. 2016). Eight elevations were sampled every 500 meters along the elevational transect (from 200 m to 3700 m), and 4 traps were positioned at each elevation, totalizing 32 collecting points covering the gradient. Specimens were collected daily and preserved in 90% ethyl alcohol. The material was sorted to family level for hemipteran suborder Auchenorrhyncha. A total of 3318 specimens representing 596 morphospecies were sorted.

To study the phylogenetic structure of communities we focused on the three most abundant and rich planthoppers families (Auchenorrhyncha, Fulgoromorpha): Cixiidae, Derbidae, and Achilidae respectively with 179, 116 and 72 specimens. All these collected specimens were identified to morphospecies and their abundances were registered, yielding a total dataset of 134 morphospecies for 367 individuals.

ALTITUDE RICHNESS ESTIMATIONS.—An estimation of the morphospecies richness at each altitude was performed in order to evaluate how representative our sampling was. We used for each altitude the number of specimens collected for each morphospecies. An individual-based abundance rarefaction curve for each elevation (see Colwell et al. 2012) was performed, using iNExtPD package in R (Hsieh et al. 2016). The S(obs), richness observed and S(est) richness estimated are provided (using Chao1 estimator).

PHYLOGENY.—Two phylogenetic analyses were conducted, one containing all taxa for which we obtained at least one molecular marker and a second, more restrictive, with at least two markers obtained for each terminal. The analyses included respectively 118 and 65 terminals, comprising 112 and 59 of the 134 morphospecies species collected along the gradient, 2 specimens identified at family level, a Tropiduchidae and a Meenoplidae (in-group), and *Cicadella viridis*, *Hindoloides bipunctata*, *Huaina inca*, *Locris rubra*, (out-group). Sequences were imported from GenBank for the four known species of the out-group (see Table 1 for accession numbers). We used three molecular markers, namely the Cytochrome Oxidase subunit 1 (CO1, 658 bp), the ribosomal 18S subunit (18S, 1359 bp) which was obtained with two set of primers and Histone 3 (H3, 340 bp), totalizing 2357 bp to generate a phylogeny.

DNA was extracted from one of the specimen legs and abdomen if needed, using DNAeasy Tissue Kit (Qiagen Inc., Hilden, Germany) and according to manufacturer's protocole. Markers were obtained by PCR using either Taq Core Kit (Qiagen) and Taq-&-Load Mastermix (MP Biomedicals Inc., Europe). The PCR cycling program includes an initial denaturation at 94°C for 10 min, denaturation of 30–40 cycles for 30s at 94°C, annealing for 30s at 45–52°C depending of the primer set (see table 1), extension for 45s at 72°C, and a final extension for 10 min at 72°C. All PCR reactions included negative controls to detect any possible contamination.

Sequences were cleaned using Codoncode Aligner 6.0.2. They were aligned using MAFFT v7.2015 (Kato & Standley 2013) for non-coding sequences such as 18S and Muscle 3.8 (Edgar 2004) for coding sequences such as CO1 and H3.

Bayesian phylogenetic inferences were performed with BEAST v1.8.2 (Drummond & Rambaut 2007), using the following parameters: Birth-death process, a lognormal uncorrelated relaxed clock, HKY model of substitution. Molecular data were partitioned by markers, each marker

being independent. Best substitution models were inferred using JMODELTEST 2.1.6 (Darriba et al. 2012), and GTR+I+G was selected on the basis of AIC for all partitions. We ran a 100.000.000 chain length and applied a 25% burn-in.

SPATIAL ANALYSIS OF COMMUNITY DIVERSITY.—A spatial analysis of community diversity was conducted with the *spacodiR* package in R (Hardy & Senterre, 2007, Hardy 2010, Eastman et al. 2011). The principle is that community phylogenetic structure can shed light on underlying processes that shape those communities, such as environmental filtering and competition, by assuming that the phylogeny of species is a proxy for traits involved in such ecological processes. Phylogenetic variance is partitioned into α (within sites) and β (among sites) component and tested using tree randomization and permutation tests (Hardy 2008). Four indices expressing community differentiation among sites for species identity (Ist) and species phylogeny (Pst, P*st and Π st) were calculated. Each index is calculated in the same way: (α -component – β -component) / α -component. Ist measures the probability that two randomly picked individuals belong to distinct species, and therefore corresponds to species turnover; Pst is the mean phylogenetic distance between individuals; P*st is the mean phylogenetic distance between individuals of distinct species; P*st > 0 indicates that communities are phylogenetically clustered, which is consistent with habitat filtering, while P*st < 0 indicates that communities are phylogenetically overdispersed, which could be the result of similarity-limiting processes, such as competition. Π st is the mean phylogenetic distance between species, without abundances information and therefore analogue to Pst (Hardy & Senterre, 2007; Hardy & Jost, 2008). We also used an additional metric, the Phylogenetic Abundance Deviation (PAD) (Hardy, 2008); $PAD = 1 - \text{mean phylogenetic distance between distinct species weighted by the product of their}$

global abundances / mean phylogenetic distance between all sampled species. PAD describes how species abundances are distributed across the phylogenetic tree.

To test the significance of the indices, we used permutation tests on the phylogeny (2-sided test, 999 randomizations, Hardy 2008), permuting all sampled species 1) on the whole phylogeny and 2) for two specified nodes: Cixiidae and Derbidae+Achilidae, in order to evaluate their respective contribution to the whole signal. Those tests were done to statistically discriminate random and clustering/overdispersion distributions. As the phylogenetic structure can be due to elevational as well as geographical distance between sites, we also performed Partial Mantel tests in order to disentangle the effects of elevational and geographic distances between sites. Permutations were conducted with *spacodiR* and Partial Mantel tests were conducted with R version 3.1.1 (R Core Team, 2014). Finally, Faith's phylogenetic diversity index PD (Faith 1992) was calculated for each site along with the mean pairwise phylogenetic distance (MPD, see Webb et al. 2002).

RESULTS

This study targets three of the most numerous families in terms of specimens and morphospecies for the Fulgoromorpha, the Cixiidae, Derbidae and Achilidae. After extraction of DNA from 134 specimens representing 134 morphospecies and performed amplification and sequencing for the three markers selected 18S, CO1 and H3, we retained two sets of morphospecies. The first one contained 112 morphospecies for which we obtained at least 1 marker and the second set contained 59 species for which we obtained at least 2 of the 3 markers. The phylogenetic analyses with the two sets of species resulted in two trees that have comparable topologies despite some slight differences. However, for the 118 (112 + 6) taxa tree neither the Cixiidae,

Achilidae or Derbidae appear as monophyletic lineages whereas for the 65 (59 + 6) taxa tree, the Cixiidae are clearly monophyletic. Here we present the results based on the phylogeny containing 65 terminals, since it is better supported (Figure 1). Sites elevation, locations and species richness observed and estimated are given in Table 2. We provide in the supplementary information the less robust 118 terminals phylogeny along with the results obtained when using it for the spatial analysis of community diversity (Figure 2 and Tables 5 and 6). These results are very similar to those obtained for the 65 terminals phylogeny.

Estimated richness roughly decreases with elevation from 700m to 3700m. it peaks at elevations between 700 and 1200m, followed by 200m, elevations between 1700 and 3200m, and is lowest at 3700m. Estimated richness differs mainly from observed richness by a higher value at 200m, probably due to bigger abundances sampled. Faith's PD tends to decrease with elevations (Table 2), with three classes of values ($PD > 200$ below 2200m, $100 < PD < 200$ between 2200m and 3200m, and $PD < 50$ above 3700m). This pattern is partly driven by species richness (PD mechanically increases as more species are added). MPD shows high values for 2200m, 2700m, and 3700m for which species richness is low. The rarefaction curves obtained for each elevation showed an asymptotic trend for elevation above 1700m (Figures 3, in the supplementary information).

PHYLOGENETIC ANALYSIS.—The in-group in the phylogeny is divided in two main clades, one that includes all the Cixiidae, another that groups the Derbidae and the Achilidae, except the terminal Derbidae 44, which is found basal to the two main clades (Figure 1). The position of the terminal Derbidae 44 is dubious and not expected. In the second clade, the Derbidae and the Achilidae form two clades, except for one Achilidae (Achilidae 58) that is basal to both clades.

The Meenoplidae specimen is also found basal and sister to all Derbidae + Achilidae to the exclusion of Derbidae 44. The Tropiduchidae is included in the clade Derbidae + Achilidae and sister to the terminal Achilidae 89. The position of the Meenoplidae, the Tropiduchidae and the distribution of Achilidae and Derbidae are however congruent with the known phylogenetic relationships within Hemiptera for the sub-order Fulgoromorpha (Urban & Cryan 2007), as Achilidae and Derbidae are not monophyletic and the relationships between these groups remain unclear. The Cixiidae appear monophyletic, like in Urban & Cryan's phylogeny (2007). In the two main clades the terminals show two different distributions according to the elevational range. The sister morphospecies of Achilidae + Derbidae tend to inhabit different elevational ranges, whereas the sister morphospecies of Cixiidae tend to share the same elevational range. At least four minor clades show this trend.

COMMUNITY PHYLOGENETIC STRUCTURE.—Across the entire dataset, the probability that two individuals from the same site belong to distinct species is $D_i\alpha = 0.8157$, the probability that two individuals from different sites belong to distinct species is $D_i\beta = 0.9910$. I_{st} is 0.1769 meaning that individuals from the same species are found more often in the same sites than in different sites (species clustering).

The mean phylogenetic distance between individuals from the same site is $D_p\alpha = 27.9510$, the mean phylogenetic distance between individuals from different sites is $D_p\beta = 39.3906$. P_{st} is 0.2904 ($p=0.0230$), meaning that phylogenetic proximity between individuals is globally higher within sites than among sites (phylogenetic clustering).

The mean phylogenetic distance between individuals of distinct species from the same site is $D_p^*\alpha = 33.3009$, the mean phylogenetic distance between individuals of distinct species from

different sites is $Dp*\beta = 39.7030$. $P*st$ is 0.1612 ($p= 0.0150$), meaning that phylogenetic proximity between individuals of distinct species is globally higher within sites than among sites. The mean phylogenetic distance between species from the same site is $DELTA\alpha = 36.8037$, the mean phylogenetic distance between species from different sites is $DELTA\beta = 40.0013$. Πst is 0.0799 ($p=0.1470$), meaning that phylogenetic proximity between species is globally higher within sites than among sites, but not significantly so.

Only Pst and $P*st$ differ statistically from the simulated values (Table 3) for the whole sample. For each clade taken individually, Pst is significantly different for Cixiidae, (0.2503, $p=0.0390$) but not for Achilidae + Derbidae (0.2809, $p=0.3270$). So the phylogenetic clustering detected in the entire dataset is driven by Cixiidae.

The phylogenetic abundance deviation for each case is positive, meaning that abundances are phylogenetically clustered even if the values are low (Table 3).

ELEVATIONAL FILTERING.—Partial Mantel tests for Pst and $P*st$ values were performed to test for correlations between elevational distances and pairwise Pst and $P*st$ while accounting for geographic distances, and vice-versa. No significant correlations were found for the whole phylogeny (Table 4) between phylogenetic distances and elevational or geographic distance. So we could not discriminate the effects of elevational and geographic distances. However, phylogenetic distances were significantly correlated with elevation for Cixiidae but not with geographic distance, when geography (resp. elevation) is accounted for. In Derbidae+Achilidae correlations are not significant.

Hence, the phylogenetic clustering can be interpreted as an elevational filtering acting on Cixiidae but not on Derbidae + Achilidae.

DISCUSSION

In this study, we generated a phylogeny of the Cixiidae, Derbidae and Achilidae collected along an elevational gradient in the Mount Wilhelm, PNG, to infer the processes that shape species assemblages from phylogenetic patterns. We selected those three families because they were the three most abundant and species-rich Fulgoromorpha groups represented in the collected material (Le Cesne et al. 2015). Therefore, we could expect them to be numerous enough to bring to light a pattern within the phylogenetic structure if any was to be observed. It was all the more essential to make such a choice as the collecting time in the field was limited and the diversity collected was only partially representative of the species number living along this altitudinal gradient. The tree topologies obtained with the two sets of data (with at least one marker, and with at least two markers) were similar, and led to similar results.

PHYLOGENY OF MOUNT WILHELM SPECIES AND FULGOROMORPHA SYSTEMATICS.—According to the current systematics of Fulgoromorpha, Cixiidae and their sister group Delphacidae are basal to Fulgoromorpha (Bourgoin et al. 1997; Urban & Cryan 2007). The next branch leads to Meenoplidae+Kinnaridae, then to Derbidae, Achilidae and Achilixiidae, for which the relationships are still unclear, while Tropiduchidae appear within the most recent lineages of the Fulgoromorpha (Urban & Cryan 2007). Our results, in terms of tree topology and relationships among the Fulgoromorpha, fit well with the current systematics (Urban & Cryan 2007). While monophyly of Cixiidae is confirmed, the Achilidae and the Derbidae are not monophyletic in our phylogeny. The position of the Meenoplidae terminal as sister to the clade Achilidae+Derbidae (except for the Derbidae 44) is congruent with the results of Urban & Cryan (2007). The position

of the Tropicuchidae included in a clade of Achilidae is not expected but could logically result from the taxon set, which lacks representatives of other groups of Fulgoromorpha.

PHYLOGENETIC CLUSTERING IN CIXIIDAE AND ELEVATIONAL FILTERING.—We found an overall pattern of phylogenetic clustering in our Fulgoromorpha dataset, but this was in fact driven by the Cixiidae. The phylogenetic structure of Derbidae+Achilidae did not depart from random expectation. Examination of the phylogenetic structure in relation with elevation further showed that the phylogenetic clustering found in Cixiidae was likely due to elevational filtering, whereby closely related species, which likely share many traits involved in adaptation to elevation-dependant conditions, such as vegetation and temperature, tend to co-occur within elevational bands. The contrasting results between Cixiidae and Derbidae+Achilidae may stem from different life-histories, with different dependence on elevation. Among the Fulgoromorpha Cixiidae is one of the largest family, most diverse in the warm-temperate and tropical regions but that can reach the Arctic Circle for a few species (Bartlett et al. 2018). Nymphs are sub-terrestrial root-feeders and adults are usually found above ground on various dicotyledonous and often woody plants. The host range of nymphs may in fact be narrower than for the adults, simply because of roots accessibility (Nickel 2003) but compared to other families of Fulgoromorpha the percentage of polyphagous species is higher (Holzinger et al. 2002). However a better knowledge of host plants is only available for species from Europe, New Zealand and North America. For the tropics most of the Cixiidae host plants remain unknown except for some occasional study such as Attié et al. (2008) in the Mascarene Islands. In the Mascarene archipelago, host plant preferences present a disparity between islands and the Cixiidae can be mainly monophagous and linked to Rubiaceae. The Derbidae are the third largest family of

Fulgoromorpha and are much more diverse in tropical than in temperate regions (Bartlett et al. 2018). Immatures are believed to be subterranean fungus feeders. Similarly to the Achilidae, the biological importance of adult host associations is not clear. The Achilidae are diverse in the tropics but are also common at higher latitudes and elevations (O'Brien 2002). The central European species are reported to live, as nymphs and adults, in fissures and under the bark of dead tree trunks, feeding on hyphae of fungi (Wilson et al., 1994; O'Brien 2002; Nickel 2003). Although the degree of host specialisation is unknown in our groups in Mount Wilhelm, difference in host use (plant roots for nymphs of Cixiidae versus fungal hyphae for Achilidae and Derbidae) could explain the contrasted phylogenetic patterns detected in those groups, and this deserves closer investigation in the future.

Other organisms show varying patterns of phylogenetic structure in both temperate and tropical ecosystems, and one of the main drivers put forward is temperature. Machac et al. (2011) studied phylogenetic patterns of ant species assemblages along an elevation gradient in three temperate montane systems, documenting contrasting patterns of overdispersion – suggesting competition – in ant communities at higher elevations, and clustering at lower elevations, suggesting environmental filtering likely driven by temperature in this case. Temperature is also one of the most important parameters segregating community assemblages in the temperate Alp Mountains for pollinating Diptera (Lefebvre et al. 2018) and for butterflies (Pellissier et al. 2013). In both cases higher elevations entail lower temperatures that filter community assemblages, leading to the presence of closely related species. Similar results have been found with Angiosperm species assemblages in Changbaishan (China) (Qian et al. 2014). Similarly, Lessard et al. (2016) found that in hummingbird communities across South America

temperature—but not precipitation or dispersal limitation—acts as the main regional filter of assemblage structure.

The main structuring forces may vary depending on the elevation considered. In bee communities along an elevational gradient in the Alps in Germany, species assemblages at high elevations is dominated by environmental filtering effect, whereas the relative importance of competition increases at low elevations (Hoiss et al. 2012). In tropical habitats, Graham et al. (2009) and Pellissier et al. (2012) found that hummingbird and bumblebee communities, respectively, tended to be phylogenetically clustered at high elevations and overdispersed at low elevations, while Chazot et al. (2014) found that phylogenetic clustering increased with elevation in neotropical butterfly communities. Furthermore, in their study involving several taxa, Bryant et al. (2008) found that microbial communities were phylogenetically clustered over all elevations, whereas plants tended to be increasingly phylogenetically overdispersed at higher elevations. The contrasting results reported in these studies suggest that different taxa have different thresholds at which abiotic factors have a filtering effect (Machac et al 2011). For instance, because butterflies are of tropical origin and tend to show climatic niche conservatism (Hawkins 2010), only a restricted number of lineages have adapted to colder environments and are able to survive at high elevations, as shown in Pellissier et al. (2013) and Chazot et al. (2014). The diversity of results among studies, and even within studies, suggests that no single mechanism is responsible for all elevational diversity gradients (Sanders & Rahbek 2012).

CONCLUSION

Our study shows phylogenetic clustering with elevation for the Cixiidae, perhaps driven by tight interactions of species in this family to hostplant along the elevational gradient. We cannot rule

out that other factors, such as temperature or precipitations, are also playing a role in filtering species assemblages. Since plants are almost unknown in the targeted region a good proxy would be to analyze adaptive traits such as rostrum morphology, as species sharing similar traits are expected to compete for similar resources (Weiher & Keddy 1995). Although we hope this work should stimulate further studies, it is only a first (but necessary) step towards a greater understanding of tropical diversity patterns and the underlying processes that shape insect communities. Clearly, a more thorough taxonomic knowledge is urgent and needed if we want to be able to manage all taxonomic levels and elaborate evolutionary scenarios.

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TABLE 1. Markers used for the phylogeny with their primers

Marker	forward primer	reverse primer	References
18S	574	E21r	Bourgoin et al. (1997)
18S	18Smid	2200r	Bourgoin et al. (1997)
CO1	LCO1490 puc +	HCO2198 puc +	
	LCO1490 hem1	HCO2198 hem1 +	Folmer et al. (1994)
		HCO2198 hem2	
H3	H3Bf	H3Br	Colgan et al. (1998)

TABLE 2. Sites, elevations, coordinates, abundances, species richness observed and estimated, Faith's Phylogenetic Diversity (PD, total branch lengths) and mean pairwise phylogenetic distance (MPD) These two last indices are based on the matrix restricted to 65 terminals

Site	Elevation (m)	Lat. S	Long. E	Abund ances	S(obs)	S(est)	Faith's PD	MPD
1	200	5.74	145.33	134	29	46.866	203.0	7.25
2	700	5.73	145.25	30	23	75.200	230.0	3.48
3	1200	5.72	145.27	21	18	53.714	247.0	3.74
4	1700	5.76	145.24	31	14	29.484	277.0	9.89
5	2200	5.76	145.19	17	8	19.765	149.0	24.83
6	2700	5.82	145.16	28	9	11.170	156.0	15.60
7	3200	5.81	145.07	27	12	17.778	173.0	3.15
8	3700	5.79	145.06	19	4	4.474	40.0	13.33

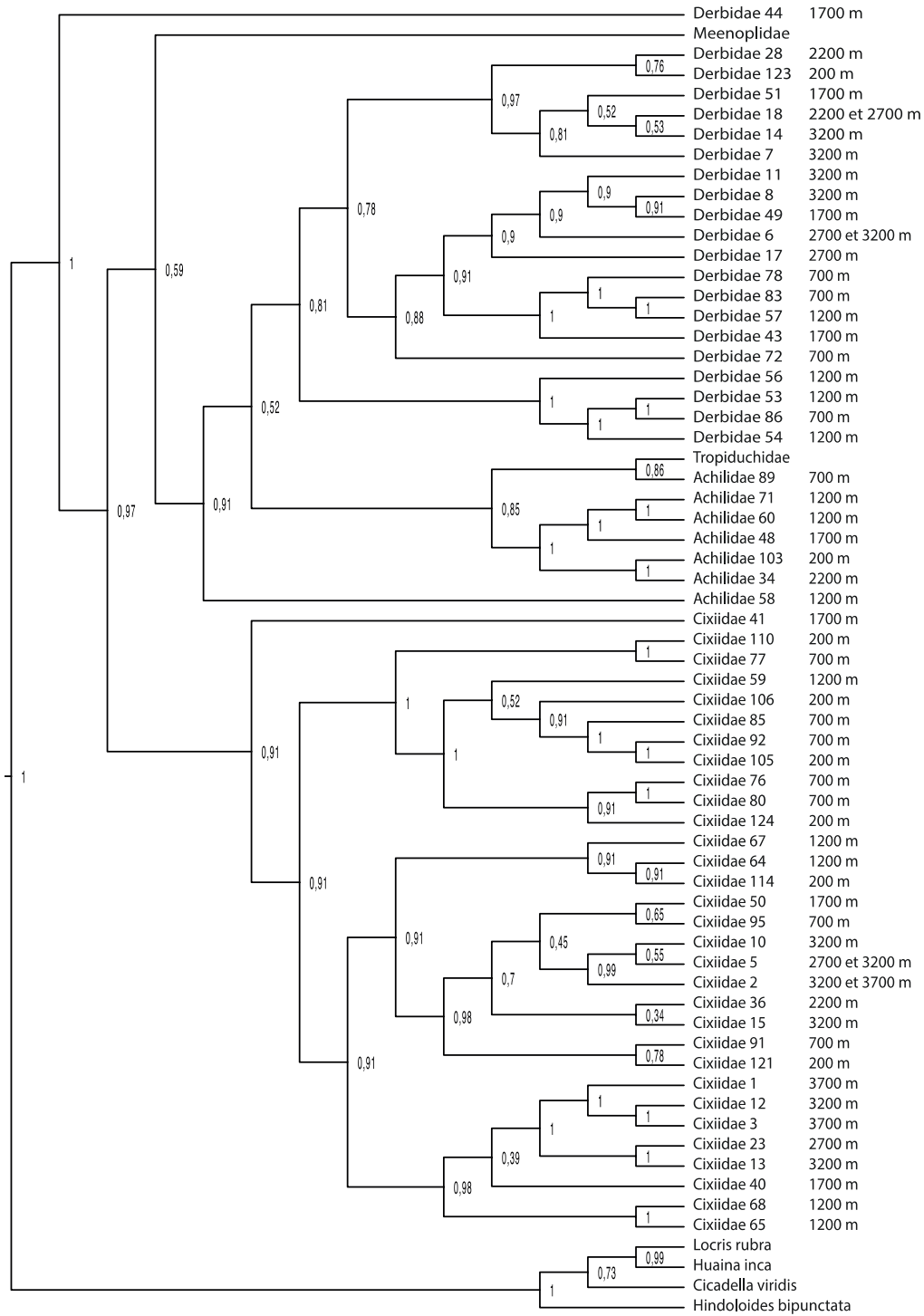
TABLE 3. Permutation tests and Phylogenetic abundance deviation (PAD) for the whole phylogeny and for Cixiidae and Derbidae+Achilidae. Observed (Obs) vs. simulated (Sim) mean permuted value, and p-value (P) given for 999 randomizations.

	Whole			Cixiidae			Derbidae+Achilidae		
	<i>Obs</i>	<i>Sim</i>	<i>P</i>	<i>Obs</i>	<i>Sim</i>	<i>P</i>	<i>Obs</i>	<i>Sim</i>	<i>P</i>
Ist	0.1769	-	-	-	-	-	-	-	-
Pst	0.2904	0.1779	0.0230	0.2904	0.2503	0.0390	0.2904	0.2809	0.3270
P*st	0.1612	0.0014	0.0150	0.1612	0.1084	0.0810	0.1612	0.1496	0.2950
Πst	0.0799	0.0005	0.1470	0.0799	0.0519	0.1870	0.0799	0.0774	0.7110
PAD	0.023597			0.066824			0.045407		

TABLE 4. Partial Mantel test's results for Pst and P*st. "altdist" is the distance matrix for mean elevation and "geodist" is the distance matrix for geographic distances. "A & B / C" means that the correlation between A and B accounting for covariate C is tested, with correlation coefficient (r_M) and p-value (P) for 999 randomizations.

	Whole		Cixiidae		Derbidae+Achilidae	
<i>Pairwise matrices</i>	r_M	<i>P</i>	r_M	<i>P</i>	r_M	<i>P</i>
Pst & altdist / geodist	0.286	0.136	0.778	0.009	0.081	0.309
Pst & geodist / altdist	-0.090	0.630	-0.641	0.981	0.379	0.080
P*st & altdist / geodist	0.302	0.117	0.676	0.018	-0.191	0.786
P*st & geodist / altdist	-0.130	0.706	-0.547	0.969	0.373	0.062

FIGURE 1. Phylogeny including 65 terminals, 59 of each belonging to the studied gradient with the altitude on which they are found



SUPPLEMENTARY INFORMATION

TABLE 5. Permutation tests and Phylogenetic abundance deviation (PAD) for the whole phylogeny and for Cixiidae and Derbidae+Achilidae. Observed (Obs) vs. simulated (Sim) mean permuted value, and p-value (P) given for 999 randomizations.

	Whole			Cixiidae			Derbidae+Achilidae		
	<i>Obs</i>	<i>Sim</i>	<i>P</i>	<i>Obs</i>	<i>Sim</i>	<i>P</i>	<i>Obs</i>	<i>Sim</i>	<i>P</i>
Ist	0.1208	-	-	-	-	-	-	-	-
Pst	0.1920	0.1215	0.0070	0.1920	0.1613	0.0470	0.1920	0.1855	0.3350
P*st	0.0877	0.0009	0.0130	0.0877	0.0553	0.1450	0.0877	0.0801	0.3550
Πst	0.0651	0.0002	0.0050	0.0651	0.0381	0.0590	0.0651	0.0552	0.0790
PAD	0.008237			0.027429			undet		

TABLE 6. Partial Mantel test's results for Pst and P*st. "altdist" is the distance matrix for mean elevation and "geodist" is the distance matrix for geographic distances. "A & B / C" means that the correlation between A and B accounting for covariate C is tested, with correlation coefficient (r_M) and p-value (P) for 999 randomizations.

	Whole		Cixiidae		Derbidae+Achilidae	
<i>Pairwise matrices</i>	r_M	<i>P</i>	r_M	<i>P</i>	r_M	<i>P</i>
Pst & altdist / geodist	0.028	0.432	-0.007	0.482	-0.081	0.654
Pst & geodist / altdist	0.133	0.264	0.351	0.045	0.370	0.096
P*st & altdist / geodist	0.015	0.451	-0.048	0.586	-0.042	0.511
P*st & geodist / altdist	0.140	0.224	0.295	0.058	0.215	0.196

FIGURE 2. Phylogeny including 118 terminals. 112 terminals belonging to the studied gradient with their elevation. Bootstrap value is given for each node

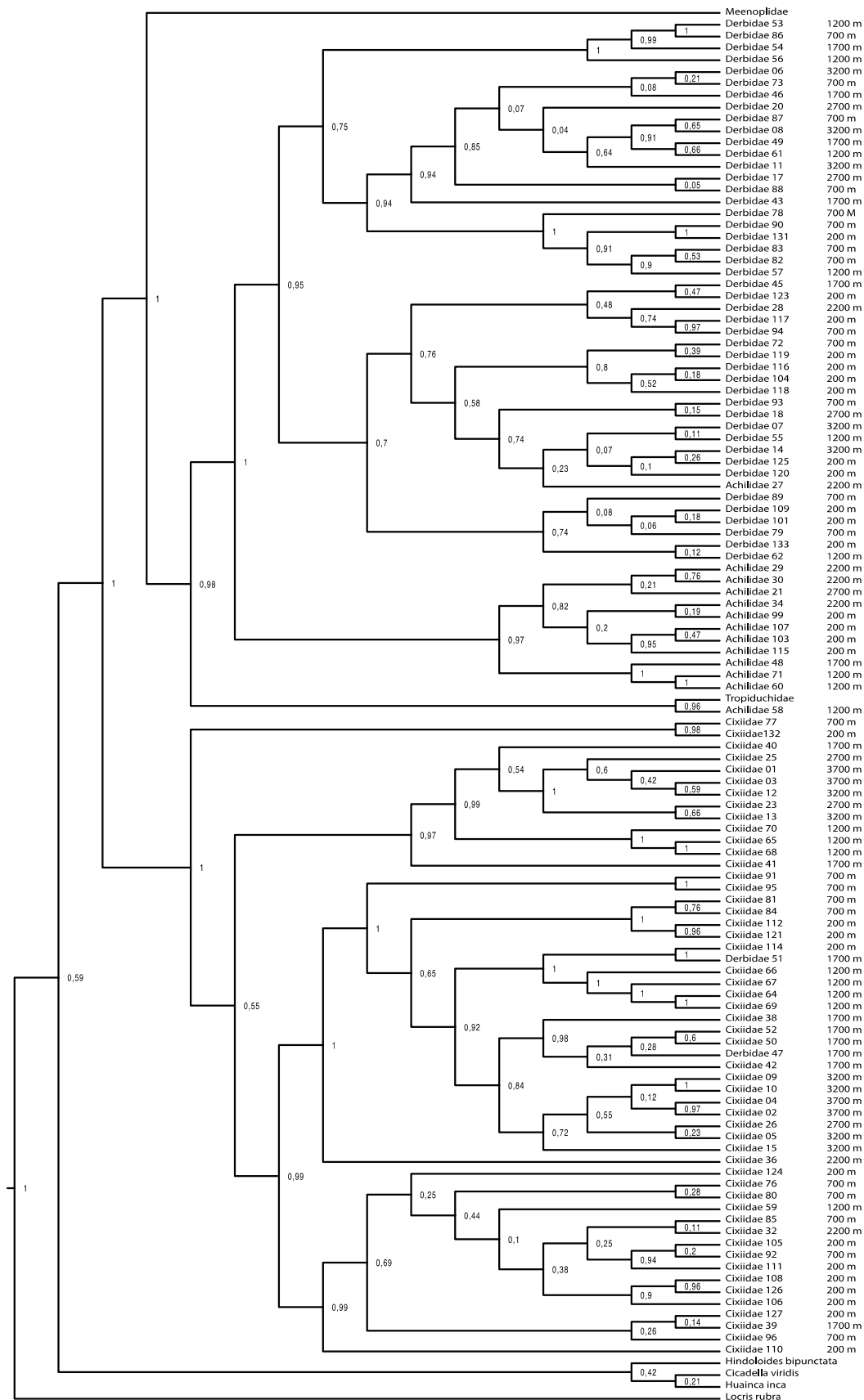


FIGURE 3. Rarefaction curves for all the elevations sampled

