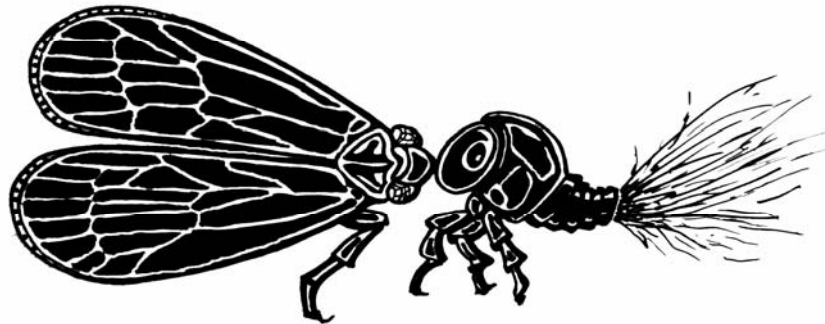# Community Structure of

Auchenorrhyncha (Insecta: Hemiptera)

Along an Altitudinal Gradient

In Papua New Guinea

FRANCESCA   FLORENCE DEM

MSc. THESIS

UNIVERSITY OF PAPUA NEW GUINEA

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NEW GUINEA BINATANG RESEARCH CENTER

A thesis submitted to the Division of Biological Sciences, University of Papua New Guinea, in part fulfillment of the requirements for the degree of Master in Science, January 2011.

Statement of Originality

I hereby declare that the material contained in this thesis is entirely my own work, except where due to accurate acknowledgement of another source has been made. Further, all the work herein was written solely for this thesis and submitted as partial completion of a Masters degree in the School of Natural and Physical Sciences, and has not been submitted for assessment in any other context.

Student signature: --------------------

Dated: 28-January- 2011

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ABSTRACT

Insect communities of tropical forests are difficult to study and are only beginning to be known, and this is particularly the case for forests of Papua New Guinea. A fundamental question asked by many ecologists is what the distributional pattern of insects along elevational gradient is. Most studies have shown that species number decreases with altitude due to unfavorable environments, low primary productivity, reduced resource diversity and reduced habitat area at high elevations. This study focuses on the distribution of auchenorrhyncha communities, including 3642 individuals and 418 species distributed among 8 localities at elevations of 200 m, 700 m, 1200 m, 1700 m, 2200 m, 2700 m, 3200 m, and 3700 m asl along an altitudinal gradient in Papua New Guinea. It is dependent on the collection of adult auchenorrhyncha by sweeping the vegetation, where 10 000 sweeps were made at each site. The number of species per 10 000 sweeps and per 200 individuals decreases with elevation. However, elevation did not affect the number of individuals. Phloem-feeders are more diverse than xylem-feeders in both the local and the whole community. The number of species per 10 000 sweeps were estimated using Chao 1 index, where the result showed that there are yet more species to be found. The number of shared and unique species distributed between adjacent sites decreases with elevation. The similarity of adjacent communities separated by 500 altitudinal m (calculated by Sorensen index) did not change with altitude. Sorensen insect similarity and Chao-Sorensen similarity for between pairs of study sites decreased with increasing altitudinal difference between sites and approached zero for more than 15000m altitudinal difference. Ordination by Canonical Correspondence Analysis (CCA) divided communities into three subgroups, the low, mid- and high elevations according to their species composition and

forest types. Most of the auchenorrhyncha species have narrow altitudinal ranges and were found either at one or two adjacent sites. The methodological problems affecting species diversity and distribution are discussed. Climate change is likely to affect insect development, reproduction and survival, and has cause insects to shift ranges upwards, resulting in extinction of those at mountaintops. This study could provide important baseline information for monitoring these changes in the future.

CHAPTER 1: INTRODUCTION

The insect communities of tropical forests are difficult to study and are only beginning to be known, as is the case for forests of Papua New Guinea. Given this paucity of knowledge, even a basic description of community structure and a search for broad correlations between community and environmental features may contribute significantly to our understanding of rainforest ecology (Janzen 1973, Janzen and Schoener 1968, Stork 1987, Wolda 1979).

A fundamental question would be: what is the pattern of distribution of insects along elevational gradients? Here are some typical examples of statements about the relationship between species richness and elevations from books and papers in major journals (Rahbek 1995). (1) "For all these reasons, we expect the number of species to decrease with altitude and, in fact it does" (MacArthur 1972, p 107). (2) "In terrestrial habitats, variation in species diversity along gradients of elevations and available soil moisture are almost as general and striking as latitudinal variation" (Brown and Gibson 1983, p 502). (3) "In terrestrial environments, a decrease in species with altitude is a phenomenon almost as widespread as a decrease with latitude"Begon *et al*. 1990, p 805). (4) "Just as change of physical conditions with altitude resembles in any respect the variation with latitude, so the decreasing in diversity of most organisms with increasing elevation mirrors in most respect the latitudinal gradient of species richness" (Brown 1988, p 62). (5) "biologists have long recognized that elevational and latitudinal species-richness gradients mirror each other" (Stevens 1992, p 899). (6) "In terrestrial ecosystems, diversity generally decreases with increasing altitude; there appear to be no substantiating data for [the] 'mid-altitudinal bulge' as a general phenomenon" (World Conservation Monitoring Centre

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1992, p 43, 45). (7) "Decrease in the number of species with decreasing temperatures at higher altitudes is as conspicuous as the decrease with latitude (e.g. Brown and Gibson 1983, although exceptions occur" (Rhode 1992, p 522). One group of studies has concluded that species richness declines with elevation. At least four reasons can be suggested for the decline (Lawton *et al.* 1987): (1) reduced habitat area at high elevations, (2) reduced resource diversity at high elevations, (3) increasingly unfavorable environments at high elevations, and (4) reduced primary productivity at high elevations. Further studies (e.g. Janzen 1973, Janzen *et al.* 1976), however, concluded that species richness peaks at middle elevations, rather than at low elevations. Two distinct processes have been proposed to explain why mid-elevations are species-rich. The first process (the "ends are bad" process) emphasizes environmental constraints on the distribution of populations. Upper limits on distributions are imposed predominantly by climatic severity and resource restriction, and lower limits mostly by climatic severity and predation (Gagne 1979, Randall 1982a, b, Young 1982, Smiley and Rank 1986). The second process (the "middle is good" process) emphasizes environmental factors that allow the species ability to gain an adaptable or competitive advantage. Photosynthetic and respiratory rates of plants are assumed to be high at low elevations and low at high elevations and, as a result, the net accumulation of photosynthate is highest at mid-elevations. The "extra" photosynthate provides a larger resource base for herbivorous insects, which in turn enable more species of both herbivorous insects and their dependent carnivores to share territory (Janzen 1973, Janzen *et al.* 1976).

Species' distributional patterns along altitudinal gradients are an important community characteristic as they are influenced by the climate in which they live. Indeed,

how climate shapes variation in the physiology, ecology, and evolution of organisms is a fundamental issue for organism biologists (Dobzhansky 1950, Andrewartha and Birch 1954, Pianka 1966, MacArthur 1972, Brown *et al*. 1996, Spicer and Gaston 1999, Chown *et al*. 2004). Biologists have long appreciated that abiotic (e.g. temperature, solar radiation, humidity) as well as biotic factors (e.g. competition, predation, parasitism) influence the conditions and the capability of an organism to survive, grow, reproduce, and disperse (e.g. Wallace 1878, Hutchinson 1957, Dobzhansky 1950, Pianka 1966, Porter and Gates 1969, MacArthur 1972, Holt 2003).

Many insect species are broadly distributed along elevational gradient, such that populations at the upper and lower gradients experience quite different environmental conditions, especially with respect to local climate. The study of the ecology of species along an altitudinal gradient may provide baseline information to the likely response of both species and communities to climate change at any one point over time. In the Janzen hypothesis (1967) "Are mountain passes higher in the tropics?" he combines these climatic and physiological considerations into a bold assumption: tropical mountain passes should be more effective barriers to dispersal than temperate-zone passes of equivalent altitude, simply because tropical organisms attempting to move up (or down) a mountain would likely encounter temperatures to which they are neither adapted nor acclimated. Many temperate studies suggest that global warming is driving species ranges poleward and towards higher elevations at temperate latitudes, but evidence for range shifts is scarce for the tropics due to lack of long term datasets (Colwell *et al*. 2008). If a similar trend were to be observed in the tropics, species living at lower elevations will move upwards, thus causing marginalization of those living particularly on mountaintops.

Any point estimation of diversity at a particular site and time made by one sampling method severely underestimates the overall diversity, as there are big differences in species composition over time (Wolda 1977), vegetation strata (Sutton 1983), individual tree canopies (Stork 1987), and different sites with similar types of vegetation (Casson and Hodkinson 1991). In addition, each method samples only a restricted part of the community (Casson and Hodkinson 1991, Wolda and Wong 1988).

This paper is devoted to the study of the community structure of Auchenorrhyncha within the forest understorey along a complete altitudinal transect in Papua New Guinea from the lowland through the montane forests to the alpine zone.

Community structural patterns along an altitudinal gradient are very important as they provide information on the species altitudinal ranges and species turnover. This study aims to document the community of Auchenorrhyncha along a forest gradient starting from 200m altitude to the sub alpine zones. The principal questions I ask are: (1) what is the total diversity of auchenorrhyncha along the entire gradient? (2) is beta diversity, i.e. turnover of species between sites constant along the entire altitudinal range or are there some sharp discontinuities in insect species composition at certain altitudes? (3) what are the differences in alpha and beta diversity among two of the three principle sap-sucking guilds; xylem- and phloem-feeders? and (4) what are the altitudinal limits of particular auchenorrhyncha species and how might they change in the future?

CHAPTER 2: METHODS

2.1. Transect establishment and Sampling sites

The study sites were established along a continuous altitudinal transect in the Bismarck
Mountain Range, starting at Kausi in Madang Province to Mt Wilhelm in the Imbuga
Range in Simbu Province. The eight sites range from 200 m to 3700 m asl at intervals of
500m (Fig.1). The sampling sites are described here in some detail to facilitate comparison
with possible future studies. The distances between adjacent sites are shown in Fig.1.
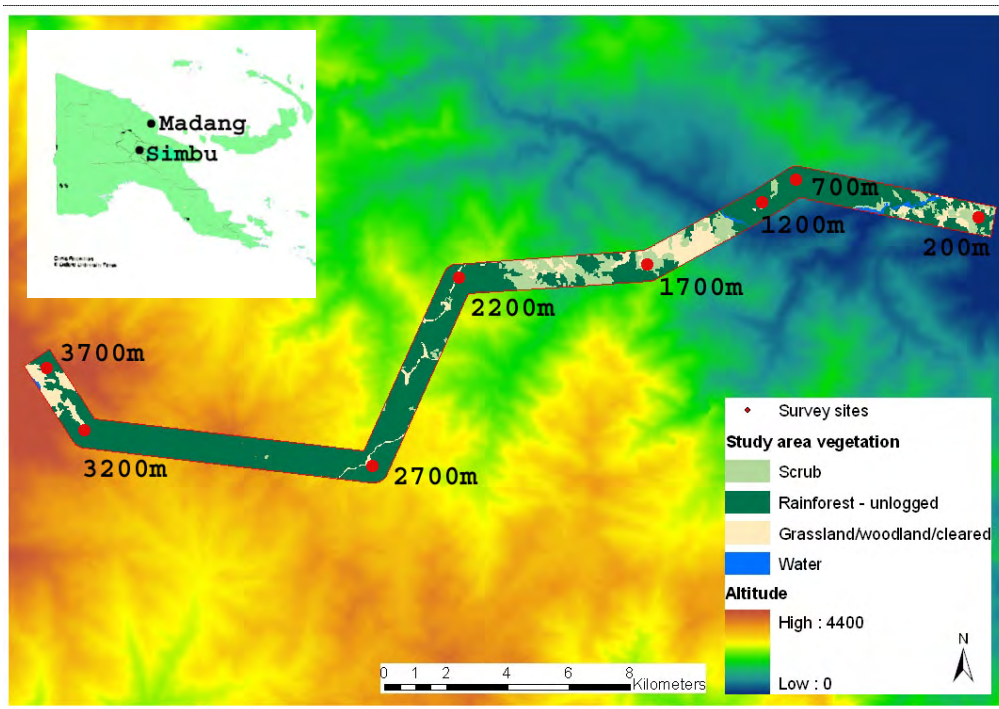

Fig.1 Altitudinal transect map showing the study sites and study area vegetation. I
divided study sites: Kausi (200 m), Bobrai-Kumi (700 m), Koviamarai-Kumi (1200 m),
Bananumbu (1700 m), Sinopass (2200 m), Kiakmangi-Bruno Sawmill (2700 m),
Kombogomambuno-Mt Wilhelm (3200 m) and Imbuga Range-Mt Wilhelm (3700 m) in
three groups according to their vegetation (Shearman *et al*. 2009).

(1) LOW ELEVATIONS: Kausi (200 m), lowland rainforest with tall canopy trees, understorey and forest floor less dense; in some sections of the forest, the forest floor is bare and the soil ploughed from pig diggings. The site is surrounded by secondary regrowth, scrub and grassland. Bobrai- Kumi (700 m), lowland rainforest with tall canopy trees, understorey and forest floor less dense. Koviamarai-Kumi (1200 m), mixture of lowland rainforest and scrub, understorey and forest floor vegetation not as dense, but partly occupied by crawling bamboo and partly by seedlings and saplings on a slope.

(2) MID-ELEVATIONS: Bananumbu-1700 m, Sinopass-2200m and Kiakmangi, Bruno Sawmill – 2700m, montane rainforest with mosses on the branches and stems of every tree and sapling and also on logs lying on the ground, generally the forest floor is covered by ground ferns. The forest is wet and damp most of the time.

The low- and mid-elevations are all located in Madang Province where the province experienced an annual precipitation of 3518mm and an annual mean temperature of 26.5 degree Celsius which is only relevant to the lowland sites. See McAlpine *et al*. (1983) for detailed climatic conditions of Papua New Guinea.

(3) HIGH-ELEVATIONS: Mt Wilhelm, Kombogo mambuno- 3200 m, a third of the area of the site is highland montane rainforest and two-thirds is open grassland with few scrubs and mostly tree ferns. Mt Wilhelm, Imbuga Range- 3700 m, the vegetation here is subalpine in which forest, grassland and mire communities form an irregular mosaic; the vegetation and plant composition are described in detail by Corlett (1984). The climatic data for 3200m and 3700m are as shown in Table 1.

Table 1: Some climatic data for the Pindaunde Field Station (3570 m), Mt Wilhelm, Papua New Guinea, from eight years of fragmentary records (Corlett 1984).

Precipitation (mm/ year)	*c*. 3450
Mean daily maximum temperature (^{O}C)	11.6
Mean daily minimum temperature (^{O} C)	4.0
Absolute maximum temperature (^{O}C)	16.7
Absolute minimum temperature (^{O}C)	- 0.8
Mean diurnal temperature range (^{O}C)	*c*. 7.0
Annual range of monthly mean minima (^{O}C)	1.6

The climate is cold and wet (Table 1). Precipitation is seasonal, but even during the drier season, rainless periods of more than a few days are rare (Corlett 1984).

2.2 Community sampling

All species of Auchenorrhyncha except Cicadellidae-Typhlocybinae are the subject of this study. This group is one of the lineages of Hemiptera, although recent analyses indicated that it may be a paraphyletic taxon (Sorensen *et al*.1995). All species of auchenorrhyncha are sap sucking herbivores, members of one of the three guilds (see Novotny and Wilson 1997 for details); (i) xylem- feeding Cercopoidea, Cicadoidea, Cicadellidae: Cicadellini (sensu Hamilton 1983) ; Cicadellinae sensu (Young 1968) and Mileewini (their position is unclear; they were treated as xylem-feeders, based on the observations from the study by Novotny and Basset (1998); (2) mesophyll-cell-feeding: Cicadellidae: Typhlocybinae; and (3) phloem-feeding: remaining Auchenorrhyncha and Sternorrhyncha. However, only two

guilds are of prime concern in the present study: (i) xylem-feeders; Cercopoidea and Cicadellidae: Cicadellini (ii) phloem-feeders; remaining Cicadormorpha and Fulgoroidea (note the present study does not include Sternorrhyncha which forms another important component of the phloem-feeding guild). As in almost any other studies, the above guilds are in fact 'taxon guilds' (*sensu* Simberloff and Dayan 1991), i.e. groups defined both by their food resource and phylogenetic lineage.

The sampling was done during two field trips of two months each where each site was sampled for ten days. The sites sampled during the first patrol started from May 27 to June 6 2009 (700 m), June 16 to June 27 2009 (1700 m), July 11 to July 21 2009, (3700 m) and July 27 to August 06 2009 (2700 m). In the second patrol, the sites sampled started from October 19 to October 28 209 (200 m), November 04 to November 11 2009 (1200 m), November 22 to December 02 2009 (2200 m) and January 20 to January 30 2010 (3200 m). Our sample demonstrates difficulties of reaching sufficient sample size for insect communities in tropical forests. Altogether 20 sampling units consisting of 500 sweeps each were made at each site. Our sweeps were performed with a circular net 30 cm in diameter and were on average 1.5 m long which means that 10 000 sweeps sampled approximately 4200 m^3 vegetation, or 1 m thick layer of under storey vegetation over 0.4 ha of forest at each site, and over 3.4 ha of forest along the entire transect, a rather substantial sample size.

2.3 Specimens dissection and identification

Leaf-hoppers and plant-hoppers from the samples were dissected and identified to morphospecies based on the external morphology as well as morphology of genitalia. As

in many insect groups including auchenorrhyncha, identification of species relies to a large extent on dissection of the male genitalia, particularly the shape of the aedeagus (Appendix 1). Identification of the samples were difficult as it is time consuming and requires a thorough check on both the physical and genitalia segment. In addition, because most of the families have very soft wings, once the wings are damaged it is very difficult trying to figure them out. The male genital segment was left in 10 % potassium hydroxide (KOH) for 24 hours, and then rinsed with ethanol. This helps to wash away muscles and other tissues that might be blocking the aedeagus from a clear view when looking at it under the microscope. The genital segment was then dissected under the microscope, photographed and sketched, and for representative specimens preserved in glycerol in a small plastic tube pinned underneath the specimen.

2.4 Data analyses

2.4.1. Community composition

Community richness is expressed as the number of species per 10 000 sweeps recorded at each elevation. Another parameter also describing community richness is the mean number of species that were obtained by rarefaction for a sub sample of 200 individuals for each site. Their relationships were expressed by regression and their significance was tested using the F-test.

Other community description parameters are the number of individuals per 10 000 sweeps recorded at each elevation and the number of individuals recorded for the total species at each site respectively. The number of individuals was transformed to square

root values and the number of species to log values for the analyses. Their relationships were tested by Pearson correlation.

Assemblages of auchenorrhyncha as well as individual guilds were analyzed for their alpha and beta diversity. I used paired t-test to see if the mean number of xylem- and phloem-feeding species differed between local communities and one-way ANOVA with Tukey test for differences among elevations. I used Minitab 15 to perform statistical tests.

Species richness on the entire altitudinal transect based on the sample size of 160 sampling units of 500 sweeps each was assessed using species accumulation curves. EstimateS 8.0 software was used to estimate the number of species based on the observed number of species (Mao Tau function) from sampling units of 500 sweeps. The Chao 1 index (Chao 2004) was used to calculate the total number of species including those species that were missed during sampling. Chao 1 index is estimated from the number of singleton species (sampled as 1 individual) and doubleton species (sampled as 2 individuals) as Chao $1 = S_{observed} + (singletons)^2 / (2x\ doubletons)$.

2.4.2 Community similarity

Beta diversity was analyzed related to the distribution of the number of shared and unique species between assemblages from different sites.

Sorensen index of similarity in EstimateS 8.0 program was used to estimate sampling similarities for comparisons between sites from different elevations. Sorensen index is based on the number of shared and unique species in compared assemblages and is calculated as Sorensen index $= 2c / (a + b)$, where c = number of species occurring in both samples, a, b = total number of species in individual samples. The proportion of

shared species among different elevations can be underestimated when the sampling of species is not complete. This bias is corrected by the Chao-Sorensen Similarity which compensates for the species missed by incomplete sampling. The relationships between similarity and altitude were tested by regression and correlation. The significance of correlation between altitude and pair-wise similarity values for all pairs of our 8 sites was tested using the Mantel Test.

Sample species composition and similarity was also related to altitude by constrained ordination (canonical correspondence analysis-CCA). Two analyses using log-transformed data on species abundance and altitude as explanatory variables were conducted. Only 67 species with abundance of 10 or more individuals were used for analyses. The significances of environmental variable (altitude) for the composition of insect assemblages were tested using the Monte Carlo permutation test. The CANOCO program was used in all computations (Ter Braak 1987).

Altitudinal distribution of species was evaluated in two different ways, as (i) altitudinal range, which quantifies the extent of altitudinal distribution of each species and is calculated as (maximum altitude –minimum altitude), and (ii) altitudinal midpoint, which quantifies the position of each species and is calculated as the (minimum altitude + maximum altitude)/ 2.

CHAPTER 3: RESULTS

3.1. Species richness and abundance

In total, 3 642 individuals and 418 morphospecies (mean = 73 species per site, SD = ±
51.4) represented by 16 families of auchenorrhyncha (Table 2) were recorded across the 8
samples for the entire transect. Cicadellidae is the most species diverse family with 44 per
cent of the morphospecies and 48 percent of the individuals, while the rest of the families
had between 1-17 % of morphospecies and individuals respectively.

Table 2: Species diversity of different families recorded.

Families	Number of morpho species	Number of individuals
Cicadellidae	185	1752
Derbidae	71	252
Cixiidae	41	198
Cercopidae	23	611
Achilidae	21	59
Aphrophoridae	15	284
Delphacidae	12	96
Membracidae	11	66
Issidae	11	25
Flatidae	11	22
Dictyopharidae	4	81
Meenoplidae	4	20
Tropiduchidae	4	9
Ricaniidae	2	8
Fulgoridae	1	156
Nogodinidae	1	1

The number of species recorded from 10 000 sweeps at each elevation showed a very strong significant correlation with altitude (r = -0.94, R^2 = 85.8%, $F_{1, 6}$ = 43.13, P<0.05, Fig.2a).This relationship is described by a liner regression, so that number of species decreases with increasing elevation. The same trend is observed for the mean numbers of species rarefied and interpolated for a sub sample of 200 individuals (r = -0.87, R^2 = 71.7%, $F_{1, 6}$=18.72, P<0.05, Fig.2b).
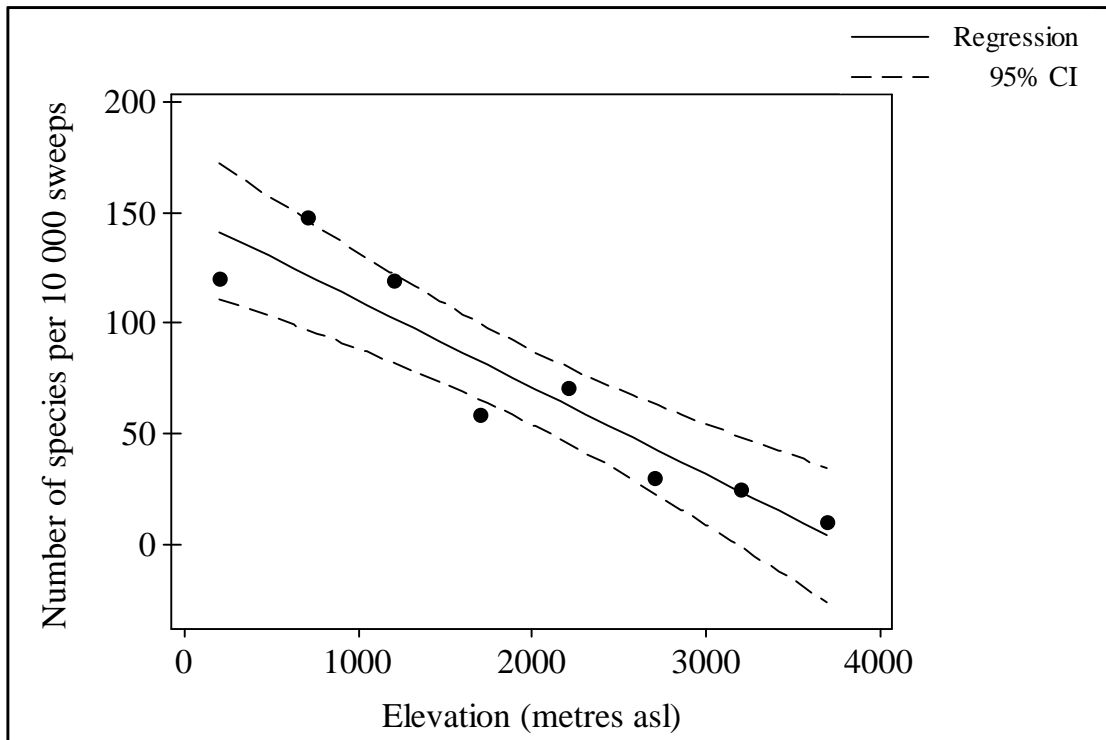
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Fig.2a: Relationship between elevation and the number of species. The two variables showed a significant correlation (r =-0.94, R^2 = 85.8 %, $F_{1, 6}$ = 43.13, P < 0.05). Each marker represents one site.
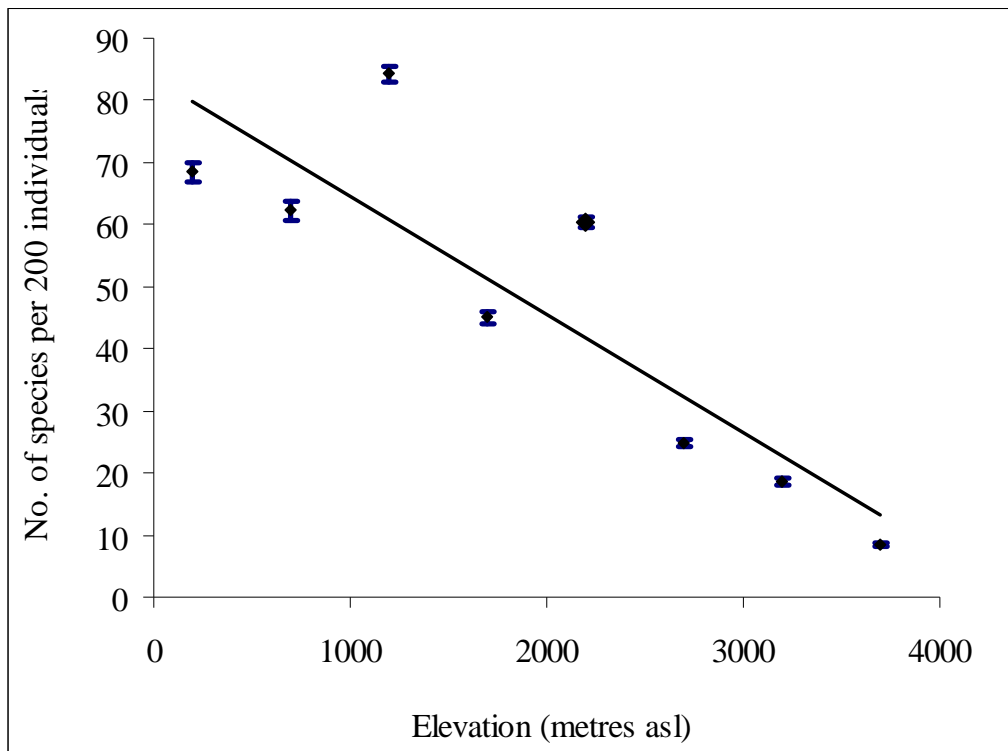
Fig. 2b: Relationship between elevation and the mean number of species at each site

There is a significant relationship between elevation and number of species (r = -0.87, R^2 =71.7%, $F_{1.6}$ = 18.72, P< 0. 05).The numbers of species were obtained by rarefaction for a sub sample of 200 individuals from given sizes. Each marker is one site and the bars represent standard errors.

The number of individuals was not correlated with elevation (Pearson correlation r = -0.657, N = 8, P>0.05, Fig. 3). This was supported by the lack of correlation between log number of individuals and log number of species (Pearson correlation r = 0.533, N = 8, P>0.05), so that in both correlations the presence of common species at a particular site mostly influenced local community population irrespective of altitude.
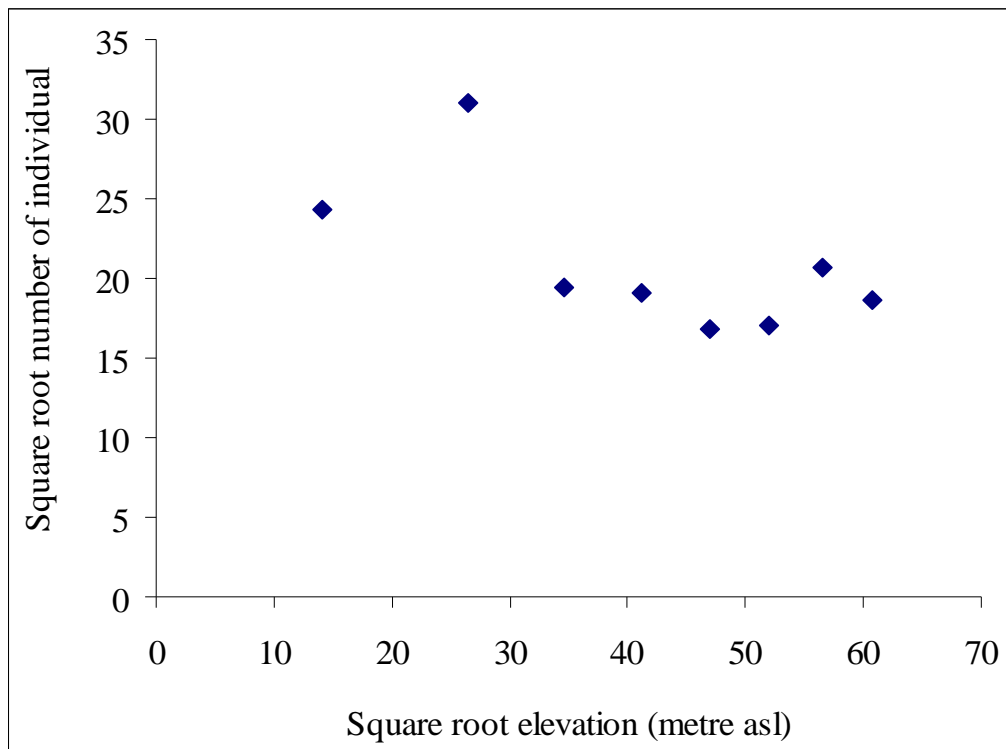
Fig. 3: Correlation between elevation and the number of individuals at each site.
There is no correlation between the two variables (Pearson correlation r = -0.657,
N = 8, P>0.05). Each marker is one site.

There are 39 species of xylem- and 379 species of phloem-feeding guilds along the
transect. Both guilds were present at all sites. Community composition of xylem- and
phloem-feeders showed that there is a significant difference in the distribution of species
between the two guilds, indicating that auchenorrhyncha assemblages are dominated by
phloem-feeders (DF = 7, Paired t-test = 3.99, P<0.05, Fig.4). Consequently, phloem-feeders
are more diverse than xylem-feeders in the pooled community (One-way ANOVA $F_{1, 14} =$
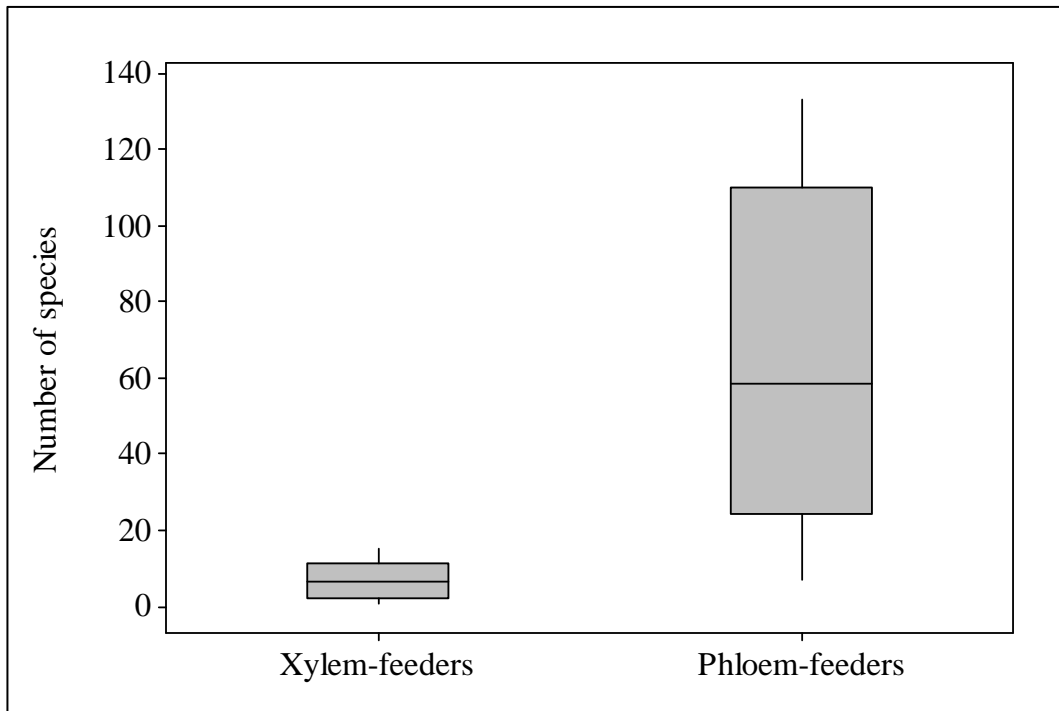12.70, P< 0.05, Fig.5).

Fig. 4: Distribution of xylem- and phloem-feeders at each site. There is a significant difference in the number of xylem-and phloem- feeders (DF = 7, Paired T-test = 3.99, P<0.05).
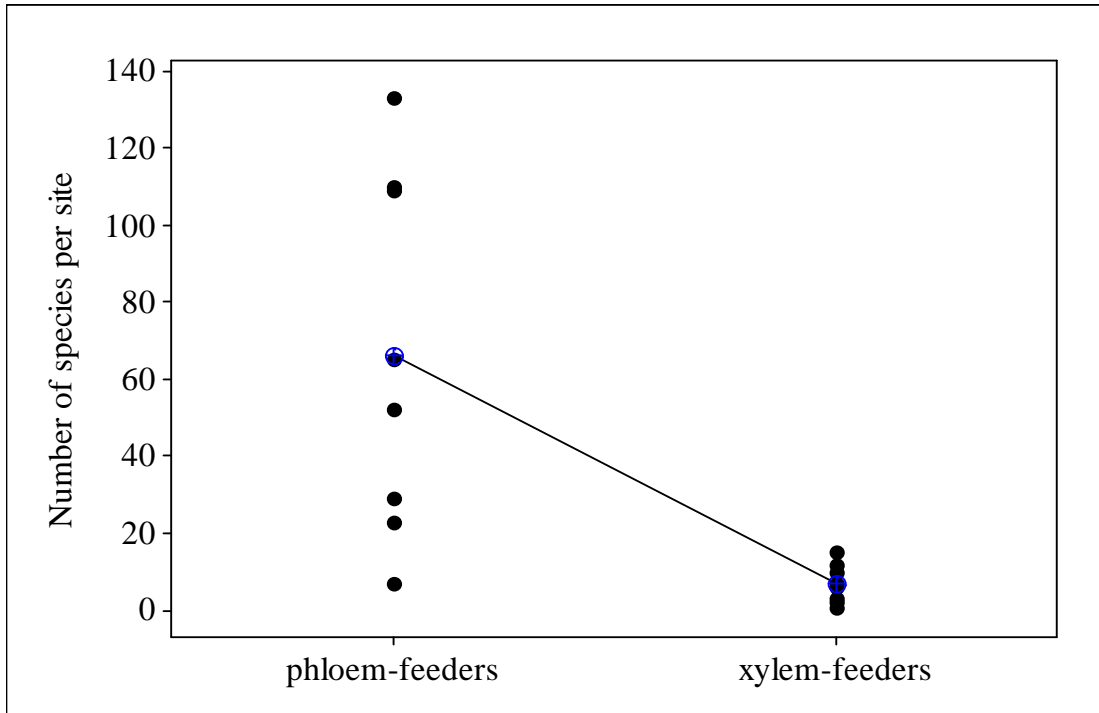
Fig.5: Distribution of xylem- and phloem-feeders among elevations. The number of species differed between the two guilds (One-way ANOVA $F_{1,14} = 12.70$, $P<0.05$). The connected markers represent the means of species number.

The dependence of species richness on sample size was explored by randomized species accumulation curves for all sampling units across all studied sites. The species accumulation curves did not reach asymptotic levels and as the estimates by Chao 1 revealed, there were at least 200 species which would have also been observed if we had larger samples sizes- perhaps even more because the Chao 1 index also did not reach an asymptote. The rapidly increasing Chao 1 values with sample size are a result of the high number of singletons and doubletons species collected in our samples.
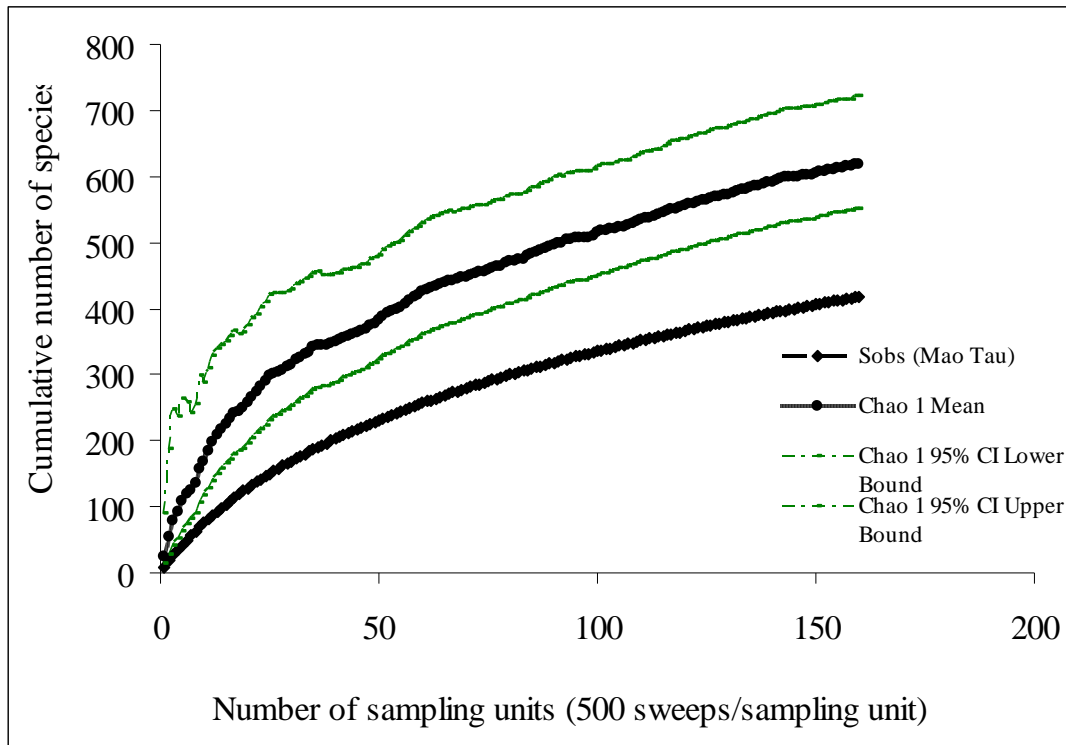
Fig.6: Species accumulation curves for the observed (Sobs Mao Tau) and the estimated

number of species (Chao 1 Mean). Samples from different sampling units were

amalgamated in random order: an average of 50 replicates is presented.

3.2. Community similarity

Beta diversity of insect species between adjacent sites are compared and described related

to the shared and unique species at low and high elevations. The number of shared and

unique species starts to decrease above the 700m x 1200m comparison (Fig.7).

Community similarity between neighboring sites as calculated by Sorensen showed

that the rate of change in species composition, particularly the proportion of shared did not

change with altitude (r = 0.323, R^2=71.7%, $F_{1, 5}$ = 0.58, P>0.05, Fig.8).
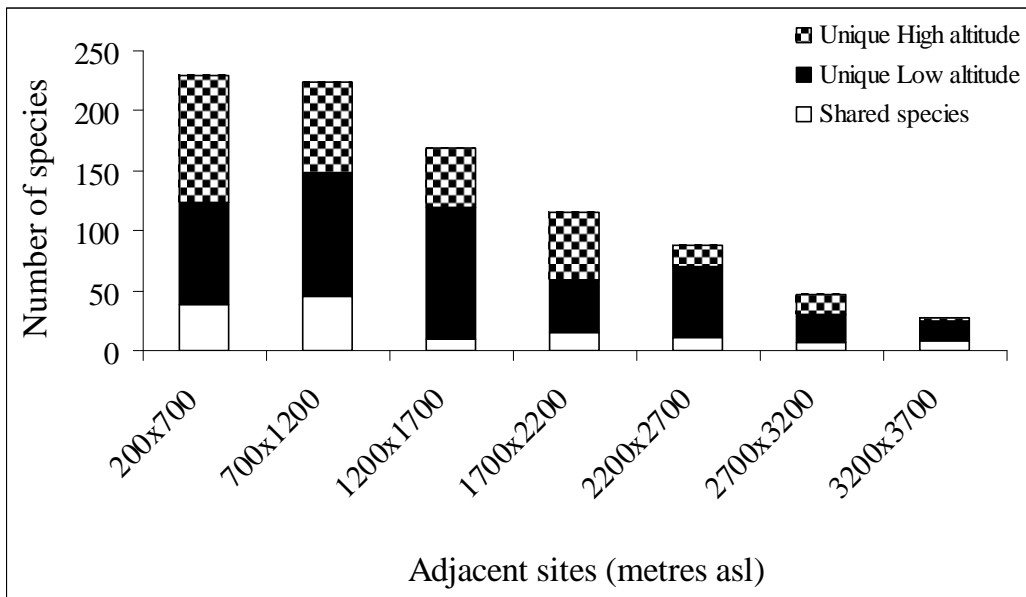
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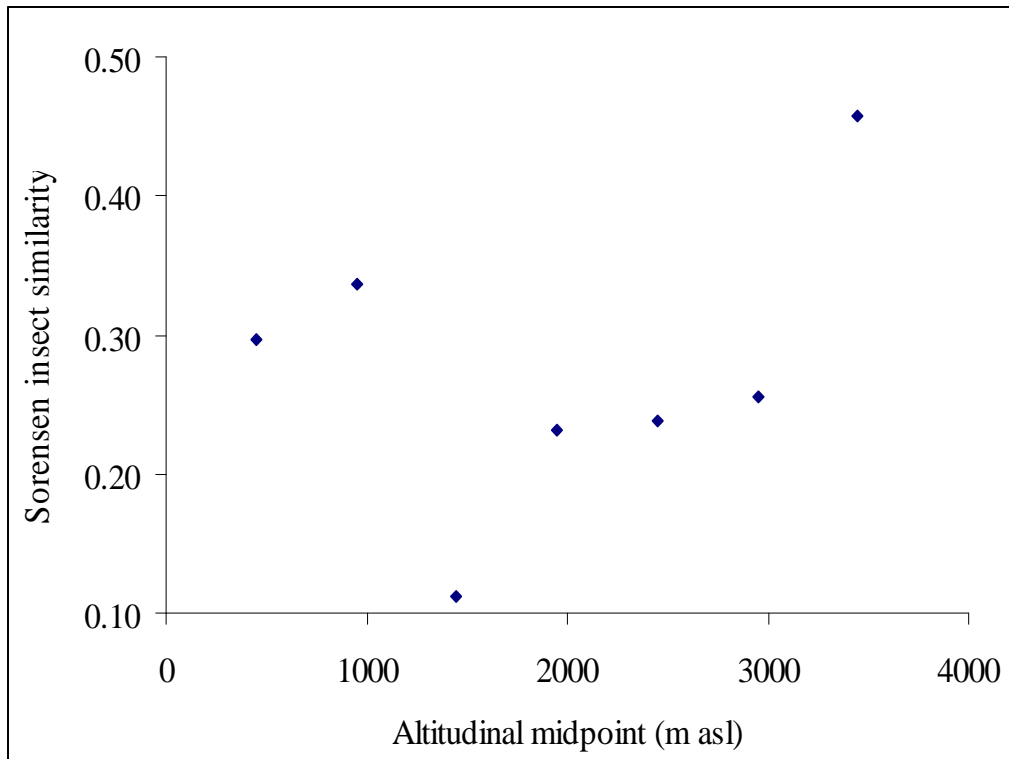
sites.

Fig.8: Relationship between Sorensen similarity of communities from neighboring sites and altitude, shown as the altitudinal midpoint between the two compared sites. Community similarity does not change with altitude (r =0.323, R^2 = 71.7%, $F_{1,5}$ = 0.58, P>0.05). Each marker is for a pair wise comparison between neighboring sites.

Insect community similarity between sites decrease as the differences in altitude increases. Insect communities closer to each other in elevation have more similar composition than those further (r = -0.48, N =28, P<0.05, Fig. 9a, Mantel test). In particular, sites 1500 altitudinal m or more apart share only very few species as their Sorensen similarity if always <0.05. Even neighboring sites only 500m elevation apart share less than 50% of species. Furthermore, Chao-Sorensen similarity which corrects for species missed during

sampling showed similar patterns, only with similarity values somewhat higher (r = -0.48, N = 28, P<0.05, Fig.9b, Mantel test).
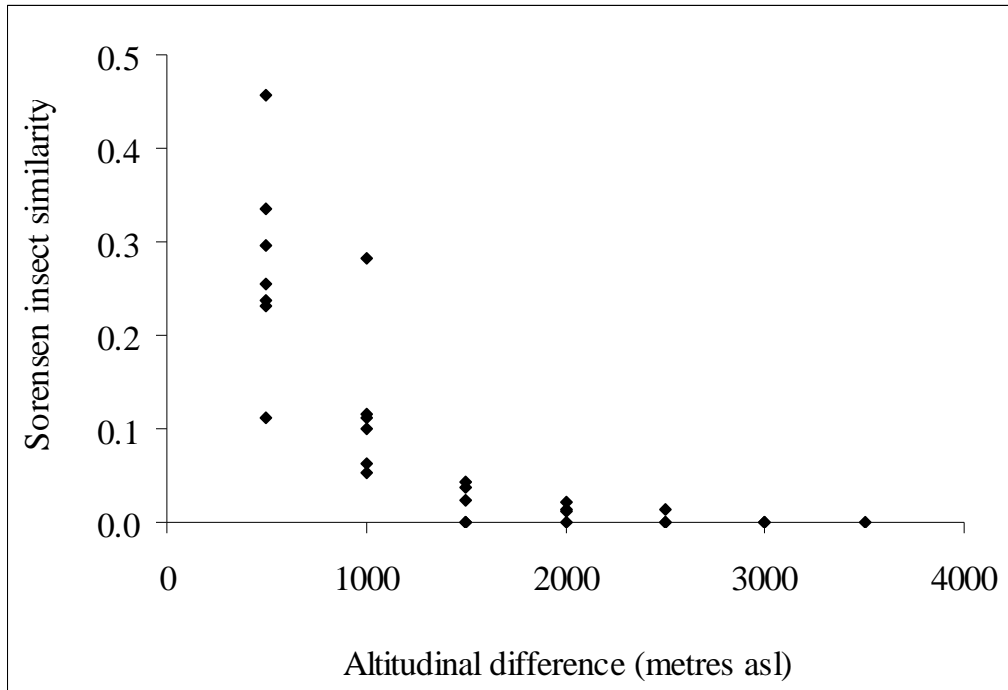

Fig.9a: Relationship between altitudinal difference and Sorensen insect similarity among studied sites at different elevations. There is a significant correlation between altitudinal difference and similarity (r = -0.47, N = 28, P<0.05, Mantel test). All pair-wise comparisons between 8 study sites were used. Each marker is one paired comparison.
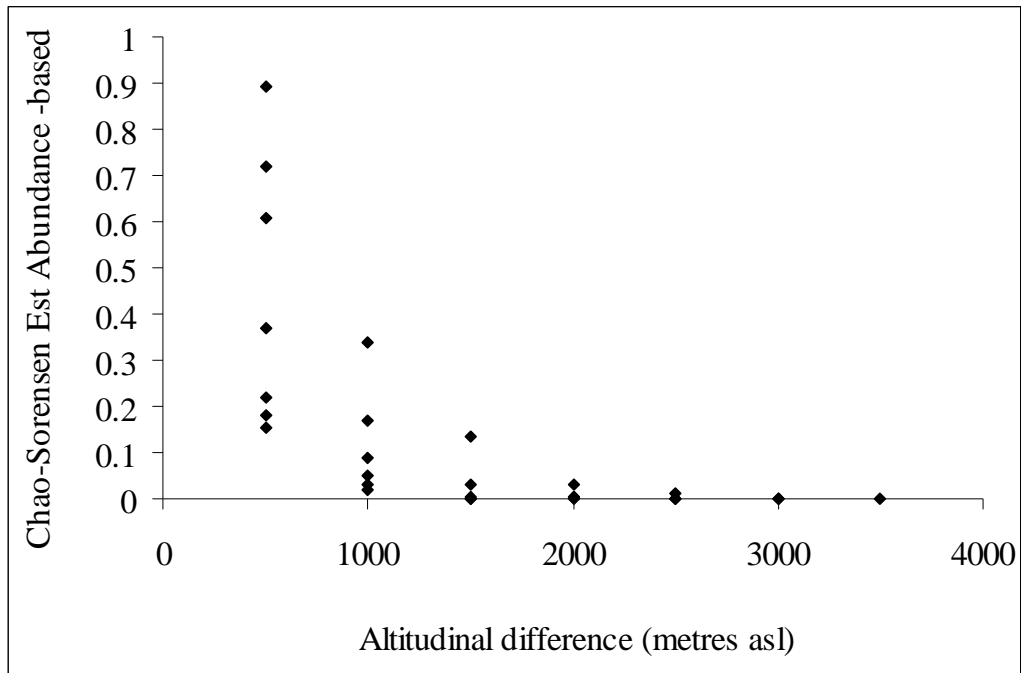
Fig.9b: Relationship between altitudinal difference and Chao- Sorensen similarity of insect communities among elevations (r = -0.48, N = 28, P<0.05, Mantel test).All pair-wise comparisons between 8 study sites were used. Each marker is one paired comparison.

As CCA ordination reveals, the auchenorrhyncha assemblages of the forest under storey along the altitudinal gradient are distinctly different from each other, forming three groups corresponding to three lowland sites, three mid-elevation sites and two high altitude sites(Figs. 10a,b). The relationship between elevation and sample composition is significant (P< 0.05, Monte Carlo method, 499 random permutations). It accounts for 46% of the sample variability as the ratio of the first and second eigenvalues (i.e. corresponding to constrained and unconstrained axes) is 0.460. The correlation coefficient between the first axis and the environmental axis is 0.983.

The forest assemblages of leaf- and plant-hoppers are further differentiated by their inter-sample distances. They may be grouped into 3 sub assemblages corresponding to groups of their study sites.
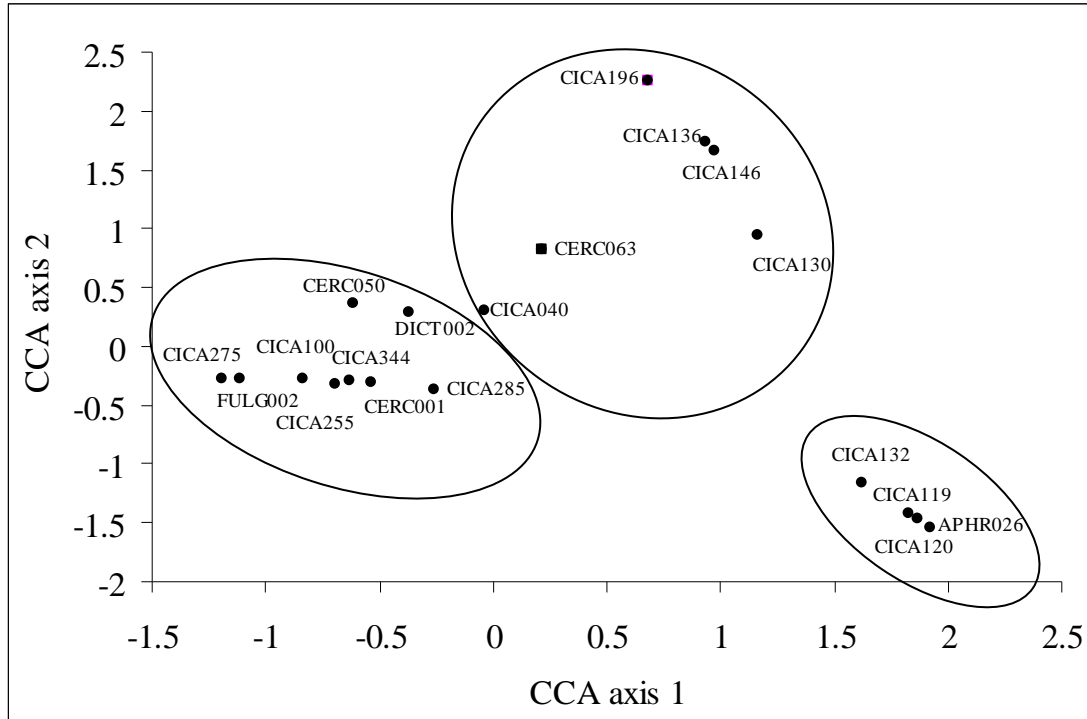

Fig.10a: Species ordination diagram with the results of CCA of the altitudinal transect. Species with 10 or more individuals were used in the analysis. The three most common species at each site are displayed on the diagram. Three groups of species correspond respectively to low-, mid- and high-elevation sites shown in Fig. 7.
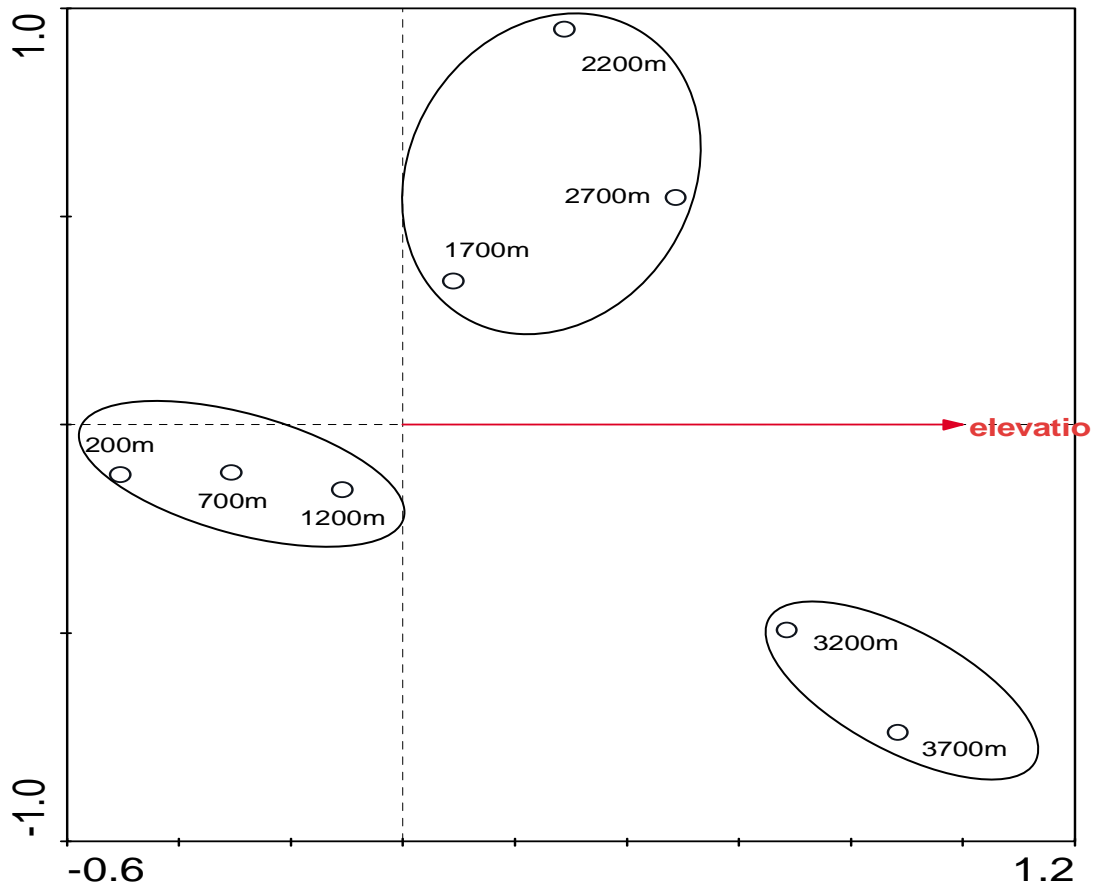
Fig. 10b: Sample- environmental variable ordination diagram with the results of CCA.

3.3. Altitudinal distribution and range size of species

The distribution of altitudinal ranges and altitudinal midpoints of species showed that most species have narrow altitudinal ranges as they were found either at a single or two adjacent sites, i.e. with a range of 0-500m (Figs.11a, b).

This is being supported by the determination of species range size expressed by the correlation of each species altitudinal range and midpoint. The correlation between the variables is not significant, so that the range size does not change with elevation (Pearson correlation r = -0.045, N = 67, P>0.05, Fig.11c).
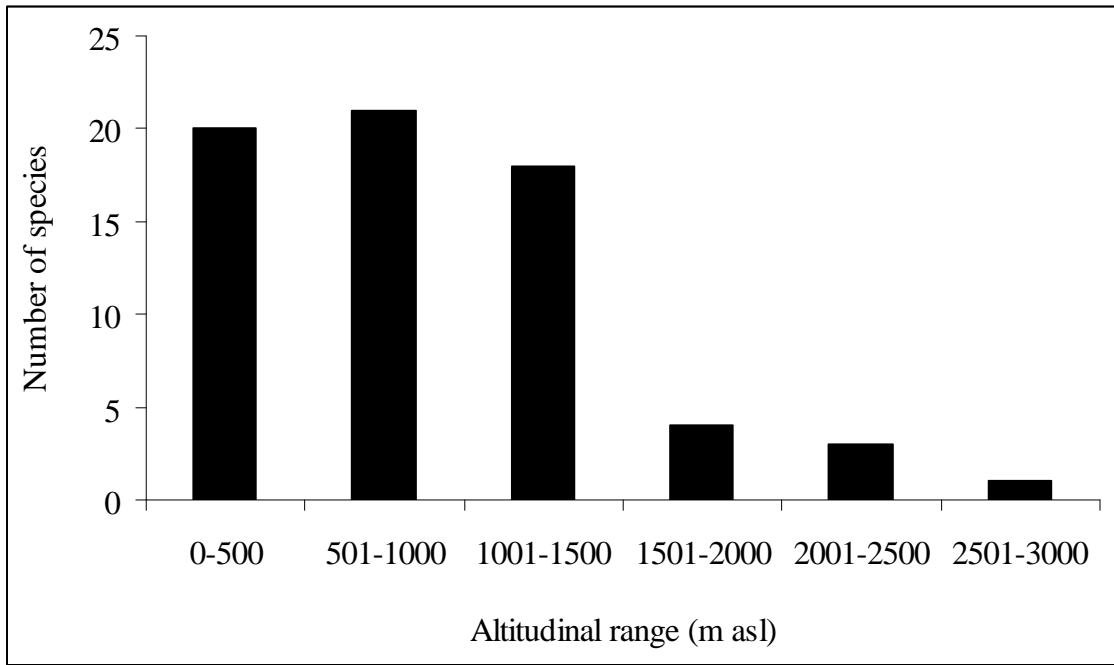
Fig.11a: Distribution of altitudinal ranges of species. Most species have narrow altitudinal ranges.

Fig.11b: Distribution of altitudinal midpoints of species. Most species have their

distribution centered on lower elevations.
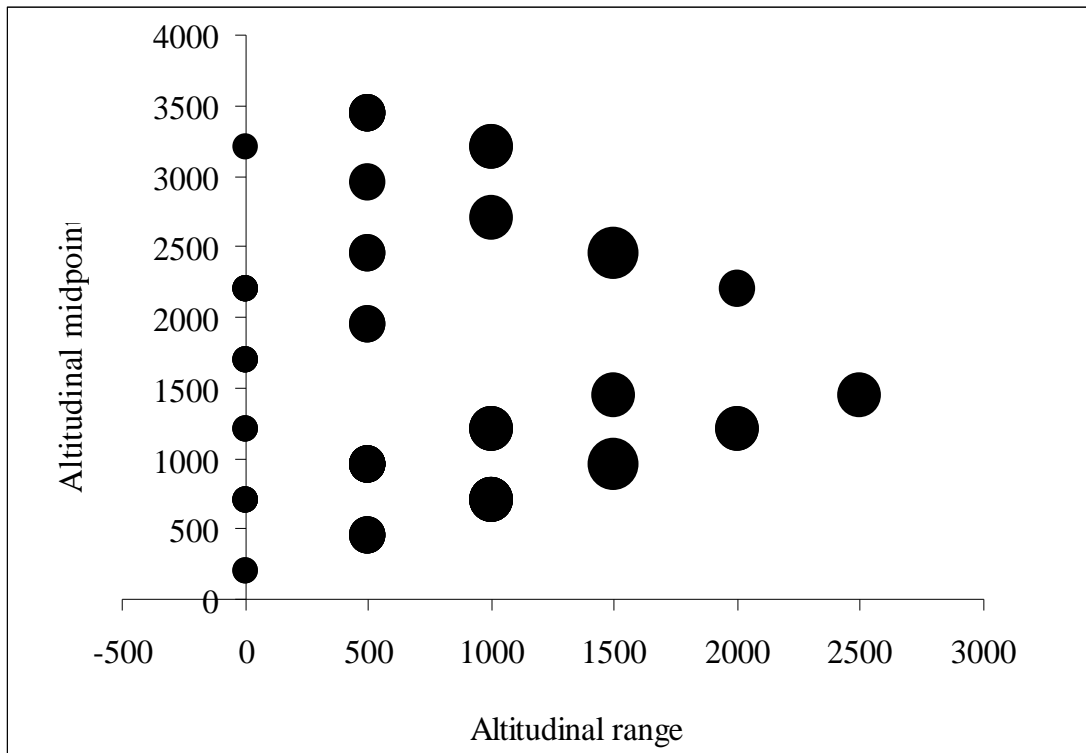
Fig.11c: Correlation between altitudinal range and altitudinal midpoint of species.

There is no significant correlation, so that species at low elevations have similar range

sizes as those at high elevations (Pearson correlation r = -0.045, N =67, P>0.05). The sizes

of the markers indicate the number of sites (from 1-4) the species is recorded.

CHAPTER 4: DISCUSSION

4.1. Species richness and abundance

The results of my sweep samples serve largely to confirm the patterns displayed in an elevational gradient as shown by other altitudinal gradient studies (as noted in Rahbek 1995). However, canopy communities which were not sampled might vary in their species composition and abundance at the different sites. This might result in a different pattern from the pattern displayed by sweep samples. The inclusion of canopy species would be made possible by light trapping. It is possible that the number of species along the gradient is mostly influenced by abiotic factors (temperature, precipitation), habitat size, primary productivity and resource availability.

With increasing elevation, temperature decreases, but most insect species prefer hot and humid atmosphere. For every 1000m increase in altitude, temperature decreases between 5.5 and 6.5 ^{o}C (Anslow and Shawn 2002) and this range has often been applied to mountain ecosystems. Local topography and conditions influence variation in temperature lapse rate (Dodson and Marks 1997; Lookingbill and Urban 2002; Rolland 2003). "Variation can result from time of the year or day, aspect, vertical atmospheric mixing and wind speed, atmospheric moisture, cloud cover and surface radiation balance"(Pepin, Benham and Taylor 1999; Pepin 2001). Precipitation is also another major factor affecting diversity and distribution of insects. At low elevations, rain as the main form of precipitation often is consistent throughout the year, which makes possible the period of insect metamorphosis short and enables numerous insects to develop and survive. Nonetheless, at higher elevations and mountain ecosystems orographic precipitation in the

form of rain, mist or dew often rises significantly along an altitudinal gradient .Although, it may rain most of the time at higher elevations, the low temperatures may hinder insects' larvae to hatch and develop.

Habitat size also determines how many species can coexist in a given square of area. As elevation increases, the area size decreases therefore only few species are able to colonize.

Primary productivity by plants tends to decrease at high elevations. At low temperatures, growth tends to be constrained more than photosynthesis (Pollack 1990; Pollack *et al*. 1984), suggesting that plants accumulate the carbohydrates for their growth and maintenance requirements, and leading to carbon-based secondary metabolites (Herms and Mattson 1992; Ayres 1993). If so, the plants growing at low temperature would be less palatable to herbivores than the foliage from plants growing at moderate temperatures (Erelli *et al*. 1998). Many plants that are fed on by the insects occupy wide altitudinal ranges. Environment differences over that range produces variation in their suitability to support insect growth and development. In particular, exposure to less favorable abiotic factors, shorter growing season and poorer soils will affect the phenology, size, morphology, physiology and chemistry with consequences for the dependent insect population (Kronfuss and Havranek 1999). Consequently, plant species growing in these unfavorable environmental conditions are less attracted by insect herbivores, therefore only a few of these insects are adapted to living in such conditions.

Different guilds showed a very significant difference in species number in both local and the pooled communities. The generalists' xylem-feeders had lower number of species as well as abundance. In support of this, observations of data sets from Novotny and

Basset (1998, 1999), Novotny and Wilson (1997) and Basset (1999) have shown that the phloem-feeders are a species-rich group compared to the other two guilds. This may be because majority of auchenorrhyncha species prefer to feed on phloem than xylem because of its nutrient levels. The hypothesis of 'energetic cost of xylem fluid extraction increases with decreasing body size as tested by Novotny and Wilson (1997) proved that xylem-feeders need a large body size in order to compensate for the amount of energy needed to extract as much xylem as possible.

On the other hand, this altitudinal pattern of species richness along elevation was not observed for abundance as shown by auchenorrhyncha. My best explanation for this is that the trends were a result of idiosyncratic, presence of a few extraordinary abundant species at each elevation such as Cercopidae species 1 at 700m and a Cicadelliade species at 3200m. McCoy (1990) showed a similar result for auchenorrhyncha except Cicadellidae displaying no relationship between abundance and elevation, however, his result on Cicadellidae alone showed a positive relationship between abundance and altitude. The possible cause of this happening is perhaps there are many rare species occurring at only some elevations or sampling was done efficiently at some sites and not others.

The species accumulation curves are still rising even after a total of 80 000 sweeps for the entire gradient. Another question we may ask if 10 000 sweeps per site is sufficient for the species- sweep curve to have leveled off. In Janzen *et al*. (1976) paper, the number of sweeps made were 800 per site which was much less than the present study, but still the asymptote was reached at 1600m. Therefore, based on this comparison my best explanations are based on the issue of sweep numbers as well as forest structure. Further, different insect taxa can differ in the proportion of rare species in their communities,

which would determine the necessary sampling size. It is clear that species-rich

Auchenorrhyncha require large sample size for the study of their communities.

Since auchenorrhyncha rely entirely on live plants for survival their biology in terms

of their ecological relationships is not discussed here as there were no data available.

However, Derbidae were probably found where there is fungi as their nymphs are

assumed to be associated with the fungi hyphae.

4.2. Community similarity

Community similarity, i.e. the proportion of shared species decreased with elevation. As

we begin to move high up the mountains, variation in environments becomes larger, as a

result community similarity decreases and therefore each community having its own

unique species.

However, with increasing altitude no differences in community similarity between

adjacent sites was observed. Environmental factors such as abiotic and plant composition

change at constant rate which resulted in a similar insect composition. A study by Andrew

and Hughes (2005) found that communities of phytophagous Hemiptera between adjacent

sites showed a high level of similarity between adjacent latitudes.

Conversely, community similarity decreases with increasing altitudinal difference as

a result of the great differences in environment variations. There are no studies on

auchenorrhyncha which have stated this otherwise, not any that I know of; however, this

may be true for insect groups such as moths. As Axmacher and his co-workers (2004)

reported, the five moth families which they studied decreased in composition with

altitude.

The proportion of variability in sample composition explained by elevation at 46 % is fairly high, thus showing a very strong gradient. Forest assemblages of auchenorrhyncha into three subgroups could be the result of differences in forest types and plant composition between the low-, mid- and high elevations. Several shared species between any two of the three subgroups tend to be inclined towards the subgroup to which they are most abundant.

4.3. Insect altitudinal distribution and potential impact of climate change

Altitudinal range size is a very important ecological characteristic as it characterizes distribution boundaries of an organism, the ability to adapt and cope with the changing microclimates and the distribution of its food resources.

The size of an organism's range determines whether/not it is able to defend itself from its enemies and escape in 'space and time'. An organism that has a wider range size has more time and a larger area to respond to changing environmental conditions, including climate change or changes in abundance and composition of its host plants or parasites and predators. As shown here, auchenorrhyncha have very narrow range size.

Mountain isolation and topography barriers make insects vulnerable when attempting to move upslope and whether they can be able to adapt and cope with the conditions of the new environment depends on the ability of each species. This is a very serious problem for many tropical species with narrow elevational ranges (Colwell *et al*. 2008). "Numerous species have shifted their ranges during the past decades" (e.g. Thomas *et al*. 2001; Parmesan and Yohe 2003). Results from most of these studies suggested that range changes were caused by climate change. Other studies have shown that many insect

species have precise climatic conditions (Karban and Strauss 2004). In the case of auchenorrhyncha, because their diversity decreases with altitude, most of the species I recorded have some space above the maximum recorded altitude which they could shift in response to global warming, for instance from low lands to mid-elevations; only the few high-altitude species will face difficulty shifting their range higher as they would encounter a small area availability.

Insects are among the groups of organisms most likely to be affected by climate change because climate has a strong direct influence on their development, reproduction and survival (Bale *et al*. 2002). Furthermore, insects have short generation times and high reproductive rates, so they are more likely to respond quicker to climate change than long-lived organisms such as plants and vertebrates. As a result, likely responses by insects include changes in phenological patterns, changes in habitat selection, and expansion and contraction of geographic and altitudinal ranges Therefore, climate change will affect species range, with expansion in some species and contraction in others, which in turn will lead to changes in regional and local diversity (Menendez 2007). Climate change will also affect insects' interactions (competition, predation and parasitism) or for herbivorous insects' host plants.

Not only do insect herbivores follow where their host plants are, but also respond to their nutrient quality. As stated earlier, plants become less palatable at low temperatures. Erelii *et al*. (1998) evaluated this hypothesis and the results from their experiments fulfilled the prediction of reduced host quality in the mountains.

So are these changes triggered by climate change already happening in Papua New Guinea? From my personal point of view, I would say that these changes are already

happening in Papua New Guinea, nevertheless not so obvious that people would realize. The landscapes and vegetation are changing, the highland areas are getting warmer and some insects living on the coast are now seen in the higher altitudes, for example, mosquitoes are already occupying the highlands region. When the people in the Porgera area were interviewed, they said the place is getting warmer. According to their categorization of the forest into three zones, the low, mid, and high since their ancestors, they mentioned that some animals and plants that used to grow in lower zones are now moving up to the next higher zone. In particular, a bird species which used to live only in the lower zone is now seen flying at the mid-zone; domesticated banana species that used to grow well in the lower section of the mid-zone can now be planted and grown well in the high zone (Jacka 2009.).

CONCLUSIONS

This study presents the first ever survey of auchenorrhyncha along a complete altitudinal gradient from the lowlands to the alpine zone in mountains with intact primary forests in Papua New Guinea. It forms the platform for further work on xylem- and phloem-feeders using sweep method or other related methods.

Unlike many other insect groups, auchenorrhyncha due to their peculiar preference of feeding on the xylem and phloem of plants, they need and rely entirely on live plants. Because of this characteristic, they make a very good subject for monitoring climate change since they have a very direct and critical relationship with their host plants, i.e. if they host plants are affected by the change in the climate they would otherwise really be affected as well.

Therefore, as this study provided some baseline information on insect diversity and distribution along the gradient, monitoring climate change using this existing information and more importantly including the plant component is recommended in the future.

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APPENDICES

Appendix 1: Some examples of the male genital section (aedeagus) of few species

AEDEAGUS from below
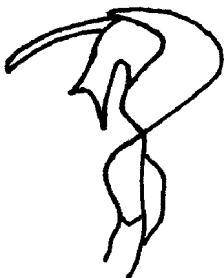
process of pygopher

AEDEAGUS from side   STYLUS
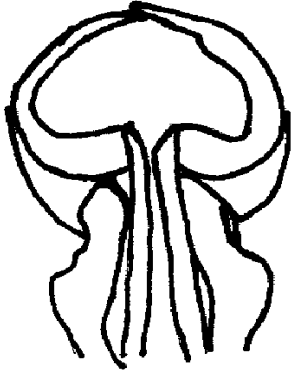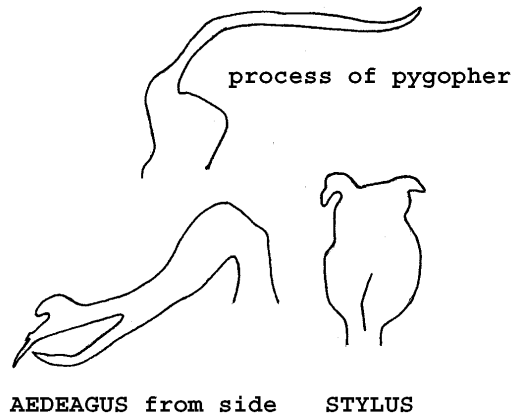
Achilidae species

Cercopidae species

AEDEAGUS from side   STYLUS
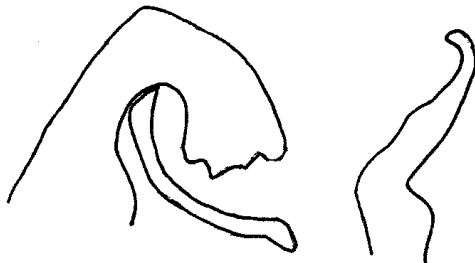
AEDEAGUS from side

Cicadellidae species

Cixiidae species

AEDEAGUS from side
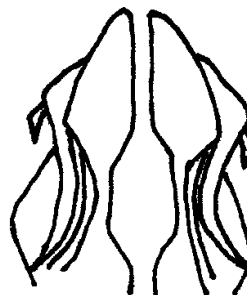
AEDEAGUS from below

Delphacidae species

Issidae species

Roguina species

Tharra rufivena

Cicadellidae species 1
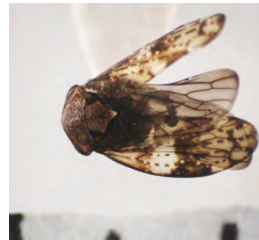
Cicadellidae species 2

Cicadellidae species 3

Membracidae species 1

Membracidae species 2

Membracidae species 3

Achilidae species 1

Achilidae species 2

Achilidae species 3

Liorhina species 1

Liorhina species 2

Liorhina species 3

Cercopidae species 1

Cercopidae species 2

Cercopidae species 3

Cercopidae species 4
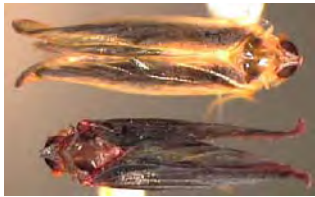
Cixiidae species 1

Cixiidae species 2

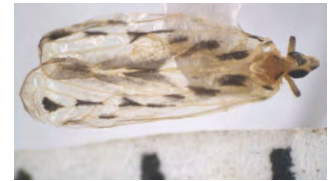*Cixiidae species 3*

Delphacidae species 1

Delphacidae species 2

Derbidae species 2
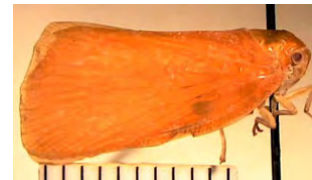
Derbiddae species 3

Derbidae species 1

Dictyopharidae species 1

Dictyopharidae species 2

Taparella amata

Colgar surrecta

Trisephena rubeola

Lieftinkana species 1

Myrilla obscura *Fulgoridae species* *Issidae species 1*

Meenoplidae species *Issidae species 2* *Issidae species 3*

Nogodinidae species *Ricania species* *Armacia hyalinata*

Tropiduchidae species 1 *Tropiduchidae species 2*