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Low host specificity in species-rich assemblages of xylem- and phloem-feeding herbivores (Auchenorrhyncha) in a New Guinea lowland rain forest

Francesca F. Dem*,†,[1], Alan J.A. Stewart‡, Amos Gibson*, George D. Weiblen§ and Vojtech Novotny*,#

* New Guinea Binatang Research Centre, PO Box 604, Madang, Papua New Guinea
† Environmental Futures Centre, Griffith University, 170 Kessels Road, Qld 4111, Australia
‡ School of Life Sciences, University of Sussex, Brighton BN1 9QG, UK
§ Department of Plant Sciences, University of Minnesota, 250 Biological Sciences Centre, 1445 Gortner Avenue, St Paul, MN 55108–1095, USA
# Biology Centre, Academy of Sciences of the Czech Republic and Faculty of Science, University of South Bohemia, Branisovska 31, 370 05 Ceske Budejovice, Czech Republic

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Abstract: We documented one of the most species-rich assemblages of tropical rain-forest Auchenorrhyncha, comprising 402 phloem- and xylem-feeding species, by sampling adults from forest vegetation. Further, we reared 106 species from larvae sampled on 14 plant species. Both xylem- and phloem-feeding guilds exhibited wide host-plant ranges, as 74% of species fed on more than one plant family. In comparison, using data extracted from the temperate-zone literature, phloem-feeders exhibited lower host specificity in Papua New Guinea than in Germany, because in Papua New Guinea they were dominated by generalist Fulgoroidea while in Germany by specialist Membracoidea. The similarity of Auchenorrhyncha assemblages from different plant species was unrelated to the phylogenetic distance between their hosts. Host specificity, abundance and species composition of Auchenorrhyncha assemblages were unrelated to the optimum of their host plant species on succession gradient from secondary to primary forest. Higher host specificity did not lead to greater species richness in Auchenorrhyncha assemblages feeding on different plant species, but the number of species feeding on a particular plant species was a strong predictor of the Auchenorrhyncha abundance on that plant. These patterns suggest that Auchenorrhyncha assemblages on these plant species are not saturated with species and determined by division of limited resources among competitors, but instead are dependent on the number of colonizers from the regional species pool.

Key Words: food web, Hemiptera, host specialization, latitudinal diversity gradient, leafhoppers, planthoppers

INTRODUCTION

Why are there so many species in the tropics? This is a deceptively simple question since the monotonous increase in diversity towards the tropics appears to be a complex result of evolutionary history and contemporary ecological interactions (Schemske *et al.* 2009). The large numbers of insect herbivores coexisting in tropical communities require an ecological explanation, pointing to the study of interspecific interactions, particularly their host specialization (Novotny & Basset 2005). The coexistence of tropical herbivores can be facilitated by their highest host specialization (Dyer *et al.* 2007), but there is currently no quantitative theory predicting latitudinal trends in species diversity for individual herbivore guilds from their host specificity. The existence of latitudinal trends in herbivore specificity remains controversial. It has been documented for Neotropical Lepidoptera (Dyer *et al.* 2007), but not for Palaeotropical leaf-chewers (Novotny *et al.* 2006). Further, more species from highly specialized herbivore guilds should

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[1] Corresponding author. Email: fdemeric@gmail.com

be able to coexist on any particular plant species than from generalist guilds. However, the empirical pattern in tropical guilds appears to be exactly the opposite (Novotny *et al.* 2012). Here we examine host specificity patterns among rain-forest trees, and contrast them with temperate zone trees, in two sap-feeding guilds and examine their importance as determinants of local and latitudinal patterns in species diversity.

There may be 10 000 herbivorous insect species feeding on 200 species of tree in a single lowland rain-forest ecosystem in New Guinea (Novotny *et al.* 2010). This extraordinary diversity is composed from multiple, ecologically distinct guilds, characterized by a broad range of host-specificity patterns (Novotny *et al.* 2010). Unfortunately, not all these guilds have received equal attention from researchers. In this respect, the contrast between leaf- and sap-feeding herbivores is particularly striking, the latter being rather neglected probably because it is difficult to verify their host plant species (Novotny & Basset 2005). Most do not cause visible damage to plants which complicates feeding experiments, and rearing their larvae to adult requires live plants for the xylem- and phloem-feeding species. This gap in our knowledge is problematic since sap-feeding herbivore lineages are species-rich and abundant on tropical plants and have potentially high, but largely unknown, impacts on their host plants, from nutrient extraction (Raven 1983) to pathogen transmission (Nault & Ammar 1989, Stafford *et al.* 2012).

A major group of sap-feeding herbivores, the leafhoppers and planthoppers (Auchenorrhyncha, Hemiptera), represent approximately 10% of all herbivore species in local assemblages on tropical tree species (Basset *et al.* 2012, Novotny *et al.* 2010). Their local diversity on mixed tropical vegetation has been estimated at 200–500 species by light and Malaise trapping, canopy fogging and sweep netting (Casson & Hodkinson 1991, Novotny 1993, Stork 1991, Sutton *et al.* 1983, Wolda 1988). While the host specificity of sap-feeding larvae has been studied in the tropics for agricultural pests (Wilson & Nault 1986, Witt & Edwards 2000), there are no quantitative studies from tropical rain forests. Here we report results of such a study, based on rearing Auchenorrhyncha larvae sampled from 14 focal tree species from a lowland rain forest in Papua New Guinea and contrasted with a temperate zone dataset from Germany. Using data from the current tropical study and the data already available from the temperate region, we addressed the following hypotheses: (1) host specialization of Auchenorrhyncha increases from the temperate to tropical areas, thus facilitating the coexistence of a higher number of species in the tropics, (2) the xylem-feeding guild is more host specific than the phloem-feeding guild, and (3) plant phylogeny is an important determinant of host plant range in Auchenorrhyncha.

METHODS

Insect sampling and rearing

All species of Auchenorrhyncha are members of one of the three sap-feeding herbivore guilds (Novotny & Wilson 1997): (1) xylem-feeding Cercopoidea, Cicadoidea, Cicadellidae: Cicadellini (sensu Hamilton 1983), Cicadellinae (sensu Young 1968) and Mileewini (their feeding guild is unclear, but they were treated as xylem-feeders, based on observations by Novotny & Basset 1998); (2) mesophyll cell-feeding Cicadellidae: Typhlocybinae; (3) phloem-feeding, which includes the remaining species. All phloem- and xylem-feeding species were sampled from above-ground vegetation; the cell-feeding guild was not part of this study as they require different rearing techniques, but is reported on elsewhere (Baje *et al.*, in review). The phloem-feeders studied here represent a taxon-guild (sensu Simberloff & Dayan 1991) since they do not include Sternorrhyncha.

The study area is situated in a mosaic of primary and secondary lowland forests near Ohu Village (145°41′E, 5°14′S, 200 m asl, Papua New Guinea (PNG) with approximately 200 tree species ha^{-1} with dbh $>$ 5 cm (Novotny *et al.* 2004). The mean annual rainfall in the area is 3600 mm with a mild dry season from July to September, mean monthly temperature ranging from 26.2°C to 26.7°C (McAlpine *et al.* 1983).

Auchenorrhyncha nymphs were sampled from 14 woody species, including three *Ficus* and one *Artocarpus* species (Moraceae), two *Macaranga* species (Euphorbiaceae), three species representing different genera of Rubiaceae, and five species representing five other families from all major lineages of plant phylogeny, including gymnosperms, basal eudicots and monocots (Gnetaceae, Monimiaceae, Ruscaceae, Myrtaceae and Sapindaceae; Appendix 1). This selection thus included both closely and distantly related species. The phylogenetic relationships among the focal plants were estimated using molecular data and methods described in Novotny *et al.* (2012).

The focal plant species represented pioneer vegetation from early secondary rain-forest succession as well as primary forest (Leps *et al.* 2001). Their distribution was surveyed in 50 plots, 20 × 20 m each. All stems with dbh >1 cm were recorded. The succession optimum index for plant species *j* was estimated as $OS_j = BAP_j/(BAP_j + BAS_j)$, where *BAP* and *BAS* is the basal area of each species in primary and secondary forest respectively.

Auchenorrhyncha nymphs were hand-collected from the focal tree species twice a week from February 2007 to July 2009, with approximately constant sampling effort throughout the study period. The studied trees were sampled from the ground or climbed. The sampling effort corresponded to approximately 1500 m^2 of foliage inspected per plant species and included numerous individual trees within approximately 500 ha of primary and secondary forests. The number of sampled trees varied from 50 to 250 individuals per species, most of them sampled repeatedly. The nymphs were collected by an aspirator and reared to adults on saplings of the same species from which they were collected. Two saplings of each host plant, 30–100 cm high, were transplanted from the forest to individual muslin cages in a shade house at the edge of the study site. Poorly performing saplings were replaced with new ones as needed. The nymphs were kept in the cages and reared adults regularly harvested from them.

Adult sap-feeding insects (Auchenorrhyncha) were also collected by hand or sweep net from accessible foliage of 13 *Ficus* (Moraceae), 12 Euphorbiaceae, two Phyllanthaceae and one Rubiaceae tree species (Appendix 1). The sampling effort was quantified only approximately, by the number of tree visits, i.e. a particular tree sampled on a particular day. The number of tree visits ranged from 20 to 355 per tree species (3761 tree visits in total) and was not kept constant among tree species. The sampling took place in the study forest of Ohu, as well as in two similar forests < 20 km apart, in Baitabag and Mis Villages. The samples were collected from July 1995 to December 1997.

Data analysis

The quantitative plant × herbivore matrix included the number of herbivore individuals from species *i* feeding on plant *j* (n_{ij}) obtained for $1, \ldots, i, \ldots, H$ herbivore and $1, \ldots i, \ldots . P$ plant species. Trophic relationships recorded as only a single reared individual ($n_{ij} = 1$) were excluded as poorly documented in the host specificity analysis. This data filtering allowed us to estimate host specificity for 35 species. Host specificity was expressed as the number of host plant species for each Auchenorrhyncha species *i* (p_i). Each herbivore assemblage on a particular plant species *j* was then characterized by the number of herbivore individuals (herbivore load, $n_{.j}$) and herbivore species (species richness, h_j). The host specificity of herbivores on plant *j* was quantified as the mean number of potential host plant species per herbivore species (HS_j) and the mean number of potential host plant species per herbivore individual:

$$HI_j = \sum_i (n_{ij} p_i)/n_{.j}.$$

The latter parameter corresponds to the host plant range expected for a herbivore individual randomly drawn from the assemblage on a particular plant species.

The number of host plant species recorded for a particular herbivore species is constrained by the number of reared individuals. We compared the observed number of hosts with the number of host species expected for the same number of individuals drawn from a large population (we used 100 000 individuals) distributed equally among all 14 studied hosts, obtained by rarefaction.

The relationships among abundance, diversity and host specificity parameters characterizing herbivore assemblages on individual plant species was explored using classical correlation with 14 focal plant species as individual data points, as well as by independent contrasts methods, taking into account phylogenetic relationships among these plant species. The latter analysis was done by Compare 4.6 software, using the phylogeny of plant species estimated from molecular data as described in Novotny *et al.* (2010). A matrix of phylogenetic distances, measured as the absolute number of nucleotide substitutions in rbcL sequences in the ultrametric tree, was calculated for all pairs of host plant species.

The similarity in herbivore species feeding on a pair of plant species was quantified by Jaccard's index $J = a/(a+b+c)$ where a is the number of herbivore species shared by both plant species, and b and c are species limited to one of them. J can be also interpreted as a host specificity index as it equals the probability that a herbivore species from the combined pool of species feeding on the two compared plant species feeds on both of them. The similarity of herbivorous communities was correlated with phylogenetic distance of their host plants, using Pearson correlation with Mantel test.

Comparative host specificity data for the temperate region was extracted from Nickel & Remane (2002) for all phloem- and xylem-feeding Auchenorrhyncha that feed partially or exclusively on trees and woody shrubs in Germany. The majority of these host-plant associations had been established by field recording of adults or nymphs on particular host plant species as opposed to the experimental rearing approach adopted here. Nevertheless, we expect the two datasets to be comparable, at least to the level of the broad generalizations that we produce here.

RESULTS

We sampled 52 087 adult Auchenorrhyncha from 389 species and 20 families from the forest vegetation. Further, we reared to adult 1853 individual nymphs from 106 species and 15 families and documented 294 plant–herbivore trophic interactions, including 156 interactions supported by more than one reared individual (Appendix 2). The combined local diversity sampled as adults or nymphs amounted to 402 species (Figure 1 a), including 350 phloem- and 52 xylem-feeding species. The Derbidae and Cicadellidae comprised

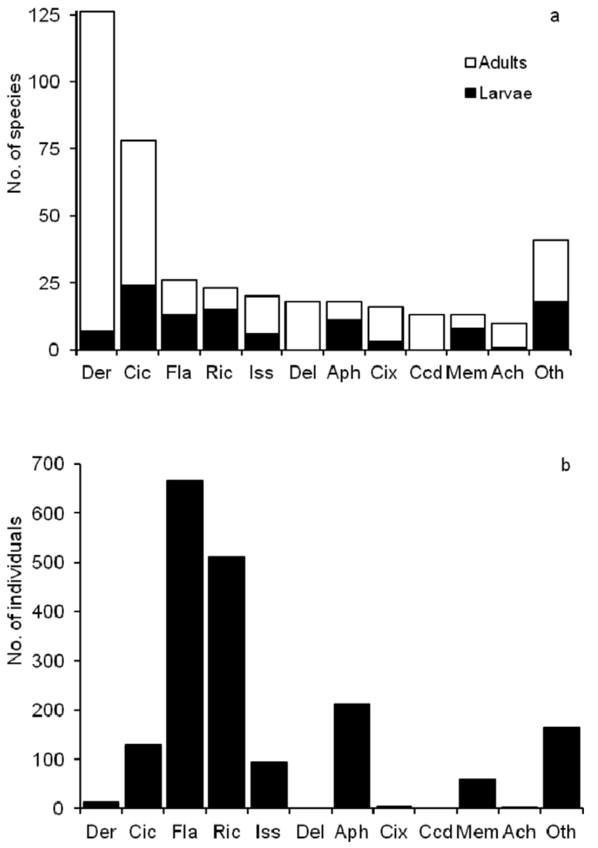

Figure 1. The number of Auchenorrhyncha species reared as larvae from 14 focal tree species and sampled as adults from 28 focal tree species (a) and the number of Auchenorrhyncha individuals reared from the focal plant species (b) in PNG. Der = Derbidae, Cic = Cicadellidae, Fla = Flatidae, Ric = Ricaniidae, Iss = Issidae, Del = Delphacidae, Aph = Aphrophoridae, Cix = Cixiidae, Ccd = Cicadidae, Mem = Membracidae, Ach = Achilidae, Oth = Other families. Sampling was conducted in the forests near Baitabag, Mis and Ohu villages in Madang, Papua New Guinea.

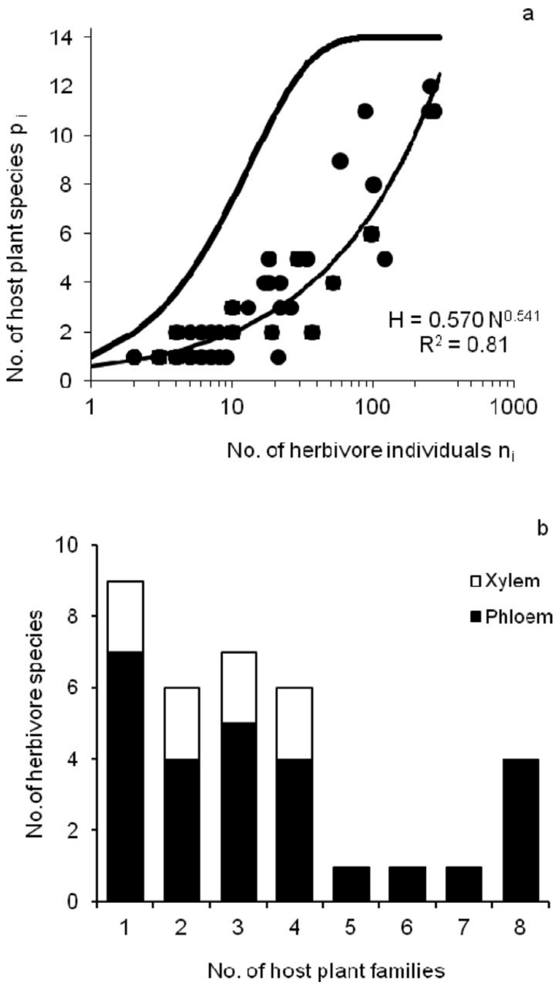

Figure 2. The relationship between the number of individuals reared and the number of host plant species recorded for Auchenorrhyncha species (a), and the number of host plant families recorded for these species, belonging either to the xylem- or the phloem-feeding guild (b). The expected number of host plant species for random distribution of individuals among the 14 studied plant species, obtained by rarefaction, is shown by the top black line. The study site is located near Ohu village in Madang, Papua New Guinea.

approximately half of all species. The reared species were mostly from Cicadellidae (22 species), Ricaniidae (15 species), Flatidae (13 species) and Aphrophoridae (11 species). The proportion of species sampled as adults and also reared from larvae varied widely among families, from zero to 65% of species in Ricaniidae (Figure 1a). The assemblages of reared individuals were numerically dominated by Flatidae and Ricaniidae (Figure 1b).

The number of host plant species increased predictably with the number of reared individuals both for xylem- and phloem-feeding species so that there were no abundant species which were also highly specialized. However, the increase in host range with the number of individuals was slower than predicted for a model assuming complete polyphagy (Figure 2 a). Both xylem- and phloem-feeding guilds exhibited wide host plant ranges, feeding typically on more than one plant family (Figure 2b). There were only nine species (i.e. 26%) specialized to a single plant family (Figure 2b).

The number of Auchenorrhyncha individuals feeding on a particular plant species ($n_{.j}$) increased with the number of species feeding on that plant (h_j), while it was not correlated with host specificity of Auchenorrhyncha (HI_j) or succession optimum (OS_j) of the host plant species (multiple regression of log $n_{.j}$ on h_j, HI_j, and OS_j, $R^2 = 0.499$, $F_{3,10} = 5.32$, $P = 0.019$, $n = 14$, Figure 3 a). This pattern was confirmed by the independent contrast analysis (multiple regression of log $n_{.j}$ on h_j, HI_j, and OS_j, $R^2 = 0.874$, $F_{3,8} = 26.4$, $P < 0.001$, $n = 12$, Figure 3b). There was no correlation between host specificity and species richness of Auchenorrhyncha

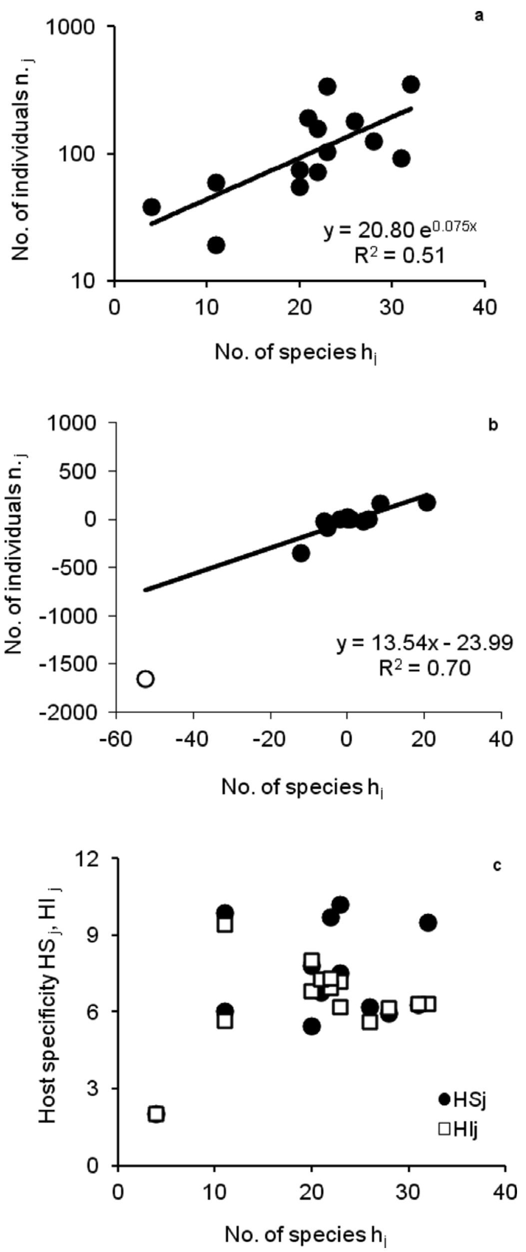

Figure 3. The relationship between the number of species in Auchenorrhyncha assemblages on the 14 focal plant species in PNG and their herbivore load analysed by classical regression, where the data points represent assemblages on individual tree species (a), their herbivore load analysed using independent contrasts based on phylogenetic relationships of the plant species (b), and host specificity (HS_j – mean number of potential host species per herbivore species, HI_j – mean number of potential host species per herbivore individual) (c). Contrast between assemblages on *Ficus bernaysii* and the remaining two *Ficus* species (open circle) was excluded from the regression as an outlier. The study was conducted near Ohu village in Madang, Papua New Guinea.

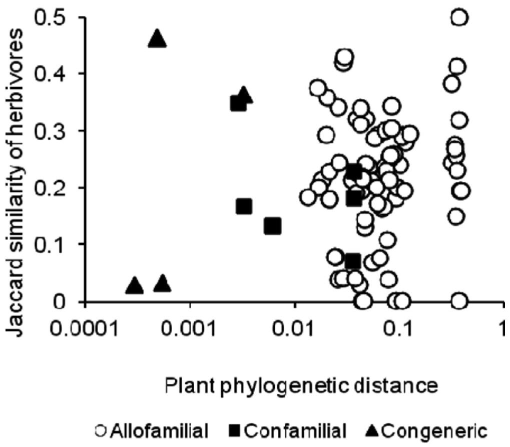

Figure 4. Relationships between phylogenetic distance of plant species and Jaccard similarity of their reared Auchenorrhyncha assemblages. All pairs of 14 plant species are shown, classified as congeneric, confamilial and allofamilial. There was no correlation between the two variables (Pearson r, P > 0.05, Mantel test). The study was carried out in the forest near Ohu Village, Madang, Papua New Guinea.

assemblages across the 14 plant species (Figure 3c, Pearson r between *h* and HI_j, P > 0.10 for both classical and independent contrast analyses). The similarity of reared Auchenorrhyncha assemblages from different host plant species was unrelated to the phylogenetic distance of these plant species (Figure 4). The similarity between Auchenorrhyncha assemblages was also unrelated to the similarity in succession optimum for their host plant species, measured as the difference between their OS_j values (Pearson r, P > 0.05, Mantel test).

The proportion of species feeding on only one plant family was higher among the 101 arboreal, phloem-feeding species occurring in Germany than among the 27 species in our PNG rain-forest communities (Figure 5). The difference in host specificity was entirely due to different relative species richness of Membracoidea and Fulgoroidea in Germany and PNG. While PNG communities were dominated by generalists Fulgoroidea, the German fauna was dominated by more specialized Membracoidea. At the same time, there was no latitudinal difference in host specificity in either Membracoidea or Fulgoroidea (Figure 5).

DISCUSSION

We have documented one of the most species-rich assemblages of adult Auchenorrhyncha on tropical rain-forest vegetation, comprising 402 phloem- and xylem-feeding species. Results for at least a further 136 mesophyll cell-feeding species (Cicadellidae: Typhlocybinae) will be published separately (Baje *et al.*, in review). Other studies of rain-forest Auchenorrhyncha reported local diversity of 300–500 species, on the basis of general sampling from diverse vegetation by

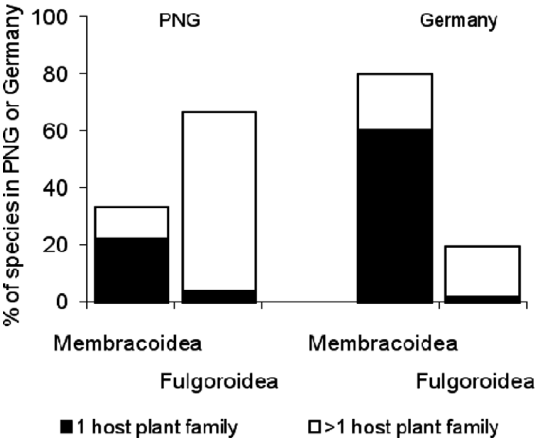

Figure 5. The taxonomic composition and host specificity of arboreal Auchenorrhyncha in PNG rain-forest communities and European regional fauna. The proportion of species feeding on 1 and >1 plant family, and recruited from the Membracoidea and Fulgoroidea lineages, are shown for the phloem-feeding species from woody plants in PNG (the present study) and in the fauna of Germany (from Nickel & Remane 2002). The total of 27 PNG and 101 German species represent 100% totals for the respective countries. The relative species richness of Membracoidea and Fulgoroidea is significantly different between PNG and Germany ($P < 0.001$, Fischer's exact test). The overall host specificity is significantly different between PNG and Germany ($P < 0.001$), but host specificity in both Membracoidea and Fulgoroidea does not differ between the two countries ($P > 0.4$, Fischer's exact test). The respective study locations are near Ohu village in Papua New Guinea and in Germany.

sweeping, fogging or light trapping (Casson & Hodkinson 1991, Novotny 1993, Stork 1991, Sutton *et al.*1983, Wolda 1988). Our sampling of adults from a limited number of focal tree species thus apparently enabled us to sample most of the local Auchenorrhyncha assemblage, comprising both species feeding on the focal trees and tourists. The fact that we were able to sample adults from a large proportion of local Auchenorrhyncha species by targeting only a fraction of local plant diversity (14 from > 200 woody species) suggests a large proportion of tourist species in our samples of adults and thus the importance of feeding experiments and rearing of larvae for the study of trophic interactions in Auchenorrhyncha, as opposed to distribution studies of adults.

Our results also support the assumption that a large part of Auchenorrhyncha diversity recorded by sampling of adults was dependent on resources other than plant foliage in the larval stage. In particular, the most species-rich family of Derbidae, as well as Achilidae, were poorly represented among reared species as their nymphs mostly feed on fungi (Wilson & O`Brien 1987) and as such should be considered as a separate guild. Cicadidae have subterranean larvae and Delphacidae feed mostly on grasses and other monocotyledoneous plants (Denno & Roderick 1990). In contrast, Cicadellidae, Flatidae, Ricaniidae and Aphrophoridae dominated the reared assemblages of Auchenorrhyncha as they all have larvae feeding on green plant parts.

The Auchenorrhyncha assemblages exhibited low host specificity. This was expected for the xylem-feeding guild which was already known for its low host specialization (Novotny & Wilson 1997), as its food resource is extremely poor in secondary metabolites as well as nutrients (Raven 1983). In contrast, phloem-feeders typically range widely from specialists to generalists. Our rearing was limited to 14 plant species, a small proportion of > 200 woody plant species present in the studied forest (V. Novotny, unpubl. data). This restricted sampling certainly missed many specialists feeding on non-sampled plants, but also additional host plants for some apparently specialized species. The relationship between host specificity estimates and sample size is complex (Novotny *et al.* 2002) so that broader sampling is needed to verify our conclusions.

The low average host specificity documented here was surprising, particularly in comparison with higher host specificity in the temperate-zone, in Germany. The Auchenorrhyncha community in PNG was dominated by Fulgoroidea while the German arboreal fauna was dominated by Membracoidea. Different representation of these taxa was entirely responsible for differences in host specificity because in both countries, Membracoidea were more specialized than Fulgoroidea. Hodkinson & Casson (2000) suggested that while small body size, coupled with high abundance, was advantageous for seeking out rare food resources, larger size and lower abundance may be associated with lower specialization. This pattern fits the difference in host specificity between relatively small and specialized Membracoidea and Fulgoroidea, which is dominated in PNG by Flatidae and Ricaniidae, known for their large body size and low host specialization (Medler 1989).

It should be noted that our tropical–temperate comparison is tentative as it contrasts local assemblages in the tropics with regional pools of Auchenorrhyncha species and their trophic interactions in the temperate zone. Standardized sampling of Auchenorrhyncha communities along latitudinal transects is needed for more detailed analyses.

The low host specificity also generated a rather unusual lack of similarity decay in herbivore assemblages with increasing phylogenetic distance between their host plant species. This was due to many Auchenorrhyncha species feeding on plant species from multiple families. Usually, phylogenetic distance between plant species is a good predictor of similarity between their herbivore assemblages, as documented for instance for caterpillar assemblages from our study site where phylogenetic distance of hosts explained 18% of variability in the assemblages of externally feeding caterpillars (Novotny *et al.* 2010).

Classical niche theory explains the coexistence of herbivorous species sharing the same host plant species by exploitation of different resources. The assemblages dominated by specialized species should thus be more species-rich than those comprising mostly generalists but this was not the case here. Furthermore, the number of Auchenorrhyncha species feeding on a particular plant species was a strong predictor of herbivore abundance. This pattern suggests that these herbivore assemblages are not saturated with species and that species coexistence on the same plant species is independent of the division of limited resources (Novotny *et al.* 2012). An increasing number of studies suggest that insect herbivore communities are rarely saturated with species and that their diversity is determined by the size of the regional species pool from which they are assembled (Caley & Schluter 1997, Harrison & Cornell 2008, Ricklefs 2004).

The position of individual plant species on the succession gradient did not explain either the species richness or host specificity of their Auchenorrhyncha assemblages. Tropical rain-forest succession is often dominated from the beginning by woody pioneer plants, which are already sufficiently apparent (sensu Feeny 1976), i.e. large and long-lived, for specialized insect herbivores (Leps *et al.* 2001). In contrast, early succession vegetation in the temperate zone comprises short-living, often annual herbaceous plants, where generalist species with good dispersal ability in Auchenorrhyncha assemblages are favoured on pioneer plant species (Novotny 1994a, 1994b).

In conclusion, xylem- and phloem-feeding Auchenorrhyncha represent an important part of herbivore assemblages on tropical vegetation. Their impact on this vegetation type remains unknown, although, judging by the pest status of many species in agricultural systems, their effects are likely to be profound. Their low host specificity makes them ideal agents for dynamically linking various unrelated plant species in the forest ecosystem, through their herbivory, potential spread of pathogens, and also as a resource for predators, parasitoids and mutualists.

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Appendix 1.

Plant species sampled for Auchenorrhyncha adults (A) and larvae (L). Euphorbiaceae: *Codiaeum ludovicianum* Airy Shaw (A), *Endospermum labios* Schodde (A), *Homalanthus novoguineensis* K. Schum. (A), *Macaranga aleuritoides* F. Muell. (AL), *Macaranga* cf. *brachytricha* Airy Shaw (A), *Macaranga densiflora* Warb. (A), *Macaranga ducis* Whitmore (A), *Macaranga novoguineensis* J.J.Sm. (A), *Macaranga quadriglandulosa* Warb. (AL), *Mallotus mollissimus* (Geisel.) Airy Shaw (A), *Melanolepis multiglandulosa* Rchb. & Zoll. (A), *Pimelodendron amboinicum* Hassk. (A); Gnetaceae: *Gnetum gnemon* L. (L); Monimiaceae: *Kibara* cf. *coriacea* (Blume) Hook.f. & Thomson (L); Moraceae: *Artocarpus camansi* Blanco (L), *Ficus bernaysii* King (AL), *Ficus botryocarpa* Miq. (A), *Ficus conocephalifolia* Ridley (A), *Ficus copiosa* Steud. (AL), *Ficus dammaropsis* Diels (A), *Ficus hispidioides* S. Moore (A), *Ficus nodosa* Teysm. & Binn. (A), *Ficus phaeosyce* Laut. & K. Schum. (AL), *Ficus pungens* Reinw. ex Blume (A), *Ficus septica* Burm. f. (A), *Ficus trachypison* K. Schum. (A), *Ficus variegata* Blume (A), *Ficus wassa* Roxb. (A); Myrtaceae: *Syzygium* sp.(L); Phyllanthaceae: *Breynia cernua* (Poir.) Muell. Arg. (A), *Phyllanthus lamprophyllus* Muell. Arg. (A); Rubiaceae: *Pavetta platyclada* K. Schum. & Lauterb. (AL), *Psychotria micralabastra* Valeton (L), *Randia schumanniana* Merr. & L.M. Perry (L); Ruscaceae: *Dracaena angustifolia* Roxb. (L); Sapindaceae: *Pometia pinnata* Forster (L).

Appendix 2. The phloem- and xylem-feeding Auchenorrhyncha species reared from the 14 focal plant species. $n_{i.}$ = number of reared individuals, p_i = number of host plant species.

Sp. Code	Species	Family	$n_{i.}$	p_i	Guild
ACHI010	Gen. & sp. indet.	Achilidae	1	1	phloem
APHR008	Gen. & sp. indet.	Aphrophoridae	1	1	xylem
APHR027	Gen. & sp. indet.	Aphrophoridae	1	1	xylem
APHR001	*Liorhina disjuncta* (Walker)	Aphrophoridae	97	6	xylem
APHR002	*Liorhina* sp.	Aphrophoridae	54	6	xylem
APHR003	*Liorhina* sp.	Aphrophoridae	21	4	xylem
APHR005	*Liorhina* sp.	Aphrophoridae	12	5	xylem
APHR006	*Liorhina* sp.	Aphrophoridae	10	2	xylem
APHR014	*Liorhina* sp.	Aphrophoridae	9	4	xylem
APHR009	*Liorhina* sp.	Aphrophoridae	1	1	xylem
APHR010	*Liorhina* sp.	Aphrophoridae	1	1	xylem
APHR004	*Liorhina suppressa* (Jbi.)	Aphrophoridae	6	3	xylem
CERC002	*Aufidus?* sp.	Cercopidae	1	1	xylem
CERC004	Gen. & sp. indet.	Cercopidae	37	2	xylem
CERC006	Gen. & sp. indet.	Cercopidae	1	1	xylem
CERC005	*Leptataspis ?discolor* Boisduval	Cercopidae	1	1	xylem
CICA028	*Conogonia sayeri* (Distant)	Cicadellidae	1	1	xylem
CICA014	*Conoguinula coeruleopennis* (F.)	Cicadellidae	1	1	xylem
CICA102	Gen. & sp. indet.	Cicadellidae	8	3	phloem
CICA129	Gen. & sp. indet.	Cicadellidae	4	1	phloem
CICA027	Gen. & sp. indet.	Cicadellidae	3	2	phloem
CICA128	Gen. & sp. indet.	Cicadellidae	1	1	phloem
CICA123	Gen. & sp. indet.	Cicadellidae	1	1	xylem
CICA004	*Kutara lucidicosta* (Walker)	Cicadellidae	22	4	phloem
CICA101	*Mileewa* sp.	Cicadellidae	1	1	xylem
CICA019	n. gen. sp. nov.	Cicadellidae	5	3	xylem
CICA013	*Nirvanguina* sp.	Cicadellidae	7	5	xylem
CICA054	*Penthimiopsis* sp. nov.	Cicadellidae	1	1	phloem
CICA001	*Philotartessus dimidiatus* (Walk.)	Cicadellidae	1	1	phloem
CICA030	*Philotartessus siautensis* F. Evans	Cicadellidae	2	2	phloem
CICA002	*Roguina* sp. nov.	Cicadellidae	32	8	xylem
CICA038	*Sarpestus* sp. nov.	Cicadellidae	6	2	phloem
CICA059	*Thagria bakeri* Nielson	Cicadellidae	7	1	phloem
CICA051	*Thagria ficta* Nielson	Cicadellidae	5	1	phloem
CICA061	*Thagria loae* Nielson	Cicadellidae	5	1	phloem
CICA016	*Thalattoscopus brunki* (Schmidt)	Cicadellidae	3	2	phloem
CICA026	*Tharra lamma* Nielson	Cicadellidae	1	1	phloem
CICA056	*Xestocephalus* sp.	Cicadellidae	2	2	phloem
CICA084	*Xestocephalus* sp.	Cicadellidae	1	1	phloem
CIXI004	Gen. & sp. indet.	Cixiidae	3	3	phloem
CIXI002	Gen. & sp. indet.	Cixiidae	1	1	phloem
CIXI024	Gen. & sp. indet.	Cixiidae	1	1	phloem
DERB091	Gen. & sp. indet.	Derbidae	1	1	phloem
DERB141	Gen. & sp. indet.	Derbidae	1	1	phloem
DERB013	*Proutista* cf. *gressitti* Van Stalle	Derbidae	5	2	phloem
DERB012	*Saccharodite?* sp.	Derbidae	1	1	phloem
DERB096	*Zoraida* sp.	Derbidae	2	2	phloem
DERB004	*Zoraida* sp.	Derbidae	1	1	phloem
DERB022	*Zoraida* sp.	Derbidae	1	1	phloem
DICT001	Gen. & sp. indet.	Dictyopharidae	18	5	phloem
DICT003	Gen. & sp. indet.	Dictyopharidae	6	3	phloem
FLAT026	*Atracis corticinus* Distant	Flatidae	1	1	phloem
FLAT005	Colgar elatum Medler	Flatidae	256	13	phloem
FLAT002	*Colgar surrecta* Melichar	Flatidae	1	1	phloem
FLAT021	*Neocromna bistriguttata* Stal	Flatidae	122	5	phloem
FLAT018	*Papuanella destituta* Medler	Flatidae	14	7	phloem
FLAT022	*Papuanella* sp.	Flatidae	2	2	phloem
FLAT029	*Paradaksha* sp. nov. nr. *furtiva* Medler	Flatidae	4	4	phloem
FLAT009	*Sephena rubrovenosa* Melichar	Flatidae	8	4	phloem
FLAT007	*Sephena* sp. nov. Medler	Flatidae	1	1	phloem

Appendix 2. Continued.

Sp. Code	Species	Family	$n_{i.}$	p_i	Guild
FLAT012	*Sephena* sp. nov. Medler	Flatidae	2	2	phloem
FLAT030	*Sephena* sp. nr. *scutellata*	Flatidae	1	1	phloem
FLAT001	*Taparella amata* Walker	Flatidae	253	12	phloem
FLAT014	*Trisephena rubeola* Medler	Flatidae	1	1	phloem
FULG001	Gen. & sp. indet.	Fulgoridae	16	6	phloem
FULG007	Gen. & sp. indet.	Fulgoridae	1	1	phloem
ISSI002	Gen. & sp. indet.	Issidae	88	12	phloem
ISSI034	Gen. & sp. indet.	Issidae	3	3	phloem
ISSI004	Gen. & sp. indet.	Issidae	1	1	phloem
ISSI015	Gen. & sp. indet.	Issidae	1	1	phloem
ISSI018	Gen. & sp. indet.	Issidae	1	1	phloem
ISSI035	Gen. & sp. indet.	Issidae	1	1	phloem
MEMB006	*Acanthucus* sp.	Membracidae	34	5	phloem
MEMB010	*Dingkana borealis* Goding	Membracidae	4	2	phloem
MEMB008	*Eufairmairia laticornis* Funkh.	Membracidae	1	1	phloem
MEMB002	Gen. & sp. indet.	Membracidae	10	2	phloem
MEMB013	Gen. & sp. indet.	Membracidae	3	2	phloem
MEMB017	Gen. & sp. indet.	Membracidae	2	2	phloem
MEMB016	Gen. & sp. indet.	Membracidae	1	1	phloem
MEMB012	*Saranthus* sp.	Membracidae	3	1	phloem
NOGO001	Gen. & sp. indet.	Nogodinidae	21	8	phloem
NOGO002	Gen. & sp. indet.	Nogodinidae	1	1	phloem
RICA004	*Armacia* cf. *hyalinata* (Donovan)	Ricaniidae	60	11	phloem
RICA003	Gen. & sp. indet.	Ricaniidae	23	9	phloem
RICA007	Gen. & sp. indet.	Ricaniidae	23	4	phloem
RICA006	Gen. & sp. indet.	Ricaniidae	11	5	phloem
RICA018	Gen. & sp. indet.	Ricaniidae	4	2	phloem
RICA001	Gen. & sp. indet.	Ricaniidae	3	2	phloem
RICA008	Gen. & sp. indet.	Ricaniidae	3	3	phloem
RICA010	Gen. & sp. indet.	Ricaniidae	2	1	phloem
RICA015	Gen. & sp. indet.	Ricaniidae	2	2	phloem
RICA019	Gen. & sp. indet.	Ricaniidae	1	1	phloem
RICA020	Gen. & sp. indet.	Ricaniidae	1	1	phloem
RICA032	Gen. & sp. indet.	Ricaniidae	1	1	phloem
RICA033	Gen. & sp. indet.	Ricaniidae	1	1	phloem
RICA002	*Ricania* sp.	Ricaniidae	273	13	phloem
RICA005	*Tarundia* cf. *glaucesenus* Melichar	Ricaniidae	103	10	phloem
TROP010	Gen. & sp. indet.	Tropiduchidae	27	4	phloem
TROP003	Gen. & sp. indet.	Tropiduchidae	21	1	phloem
TROP007	Gen. & sp. indet.	Tropiduchidae	2	2	phloem
TROP001	Gen. & sp. indet.	Tropiduchidae	1	1	phloem
TROP002	Gen. & sp. indet.	Tropiduchidae	1	1	phloem
TROP004	Gen. & sp. indet.	Tropiduchidae	1	1	phloem
TROP005	Gen. & sp. indet.	Tropiduchidae	1	1	phloem