

A test of concordance in community structure between leafhoppers and grasslands in the central Tien Shan Mountains

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Abstract Leafhoppers and related Auchenorrhynchos Hemiptera (AH) are among the most diverse grassland herbivores, and many have been linked inexorably to grassland vegetation through diet and shelter for millions of years. Are AH–plant communities in natural grasslands tightly integrated, how does the interaction differ across major ecological gradients, and do habitat or environmental factors explain the most variance in AH community structure? These questions have implications for the conservation of biodiversity and in evaluating effects of a warming climate. Using grasslands of the central Tien Shan Mountains as a natural laboratory, we examine whether AH species assemblages are concordant with vegetation in terms of community structure using closely associated species-level samples. Data were recorded from a nearly 3000-m elevation gradient crossing four arid and three montane grassland vegetation classes. We found elements of AH–plant community classification and structure to be closely correlated except for at the arid–montane habitat transition where a small group of widespread AH species were significant indicators for vegetation classes in both major grassland types. AH species richness and abundance are positively correlated with plant species density and percent cover and, correspondingly, peak at mid-elevations

in association with montane grasslands. While overall elevation (and covariate mean annual temperature) explains the most variance in AH species assemblages, the sum total of habitat factors explain more variance than environmental factors when arid and montane grasslands were examined separately, but environmental factors are co-equal with habitat factors when the grassland types are combined. Unexplained variance in the AH community assemblages, attributable to individualistic species responses to environmental and habitat factors, slightly exceeds the total accounted for by the model.

Keywords Auchenorrhyncha · Plant–insect interactions · Species density · Steppe · Central Asia

Introduction

Patterns of species composition, richness, and abundance across elevational gradients have been the focus of extensive ecological study to gain insights to factors influencing biodiversity and species interactions (reviewed in Sundqvist et al. 2013). While mid-elevational peaks of species richness and decline at higher elevations have been widely documented (e.g., Whittaker 1960; Lomolino 2001), variance in the general pattern abounds due to differences in group responses to confounding environmental factors, sampling effects, and species interactions (McCoy 1990, Rahbek 1995; Hodkinson 2005; Körner 2007). The strength of species interactions, as described for latitudinal gradients (Schemske et al. 2009), also can be altered due to changes in host susceptibility and genetic variability (Singer and Parmesan 1993; Pellisier et al. 2012).

Species range shifts with climate change also can be expected to disrupt species interactions (Rasmann et al.

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2014a). For example, insects including herbivores generally can be expected to respond to altered environmental conditions more rapidly than host plants (Hodknison and Bird 1998; Menéndez 2007). Herbivore insects with diapause, particularly those with brachypterous (flightless) forms, may be among species that could be expected to respond unfavorably to a warming climate (Hodkinson 2005). An examination of Auchenorrhyncha (Hemiptera) species assemblages, insects with diapause and variable wing lengths, recorded widely throughout a mountainous grassland ecosystem could yield insights to how species interactions change along principle ecological gradients with implications for interpreting effects of climate change.

Auchenorrhyncha

Leafhoppers and related Auchenorrhynchous Hemiptera (AH) comprise one of the most diverse and abundant groups of grassland insects (Morris 1971; Waloff 1980). These include species that appear to be monophagous or feed only on a few closely related grass species while others feed on a variety of herbaceous plants common in grassland ecosystems (DeLong 1948; Brown et al. 1992; Whitcomb et al. 1987; Whitcomb and Hicks 1988; Nickel and Remane 2002). Recent phylogenetic studies indicate that some lineages have been associated with grasses (as host plants) and grasslands (as habitats) for tens of millions of years (Zahniser and Dietrich 2010, 2013; Catanach 2013). The origin and spread of grasslands during the Oligocene and Miocene (15–25 million years ago) likely played a major role in the evolutionary diversification of leafhopper species (Dietrich et al. 1997; Dietrich 1999; Catanach 2013). Due to their numerical abundance, sensitivity to habitat conditions, and functional importance, Auchenorrhyncha species assemblages are considered a reliable indicator of habitat condition, particularly in grassland ecosystems (Hollier et al. 1994; Hamilton 1995; Nickel and Hildebrandt 2003; Biedermann et al. 2005; Maczey et al. 2005; Wallner et al. 2013a, b; Primi et al. 2016). This close ecological and evolutionary relationship (Nault and DeLong 1980; Whitcomb et al. 1987; Dietrich et al. 1997) serves as an ideal framework for examining the roles of habitat and environmental factors in community organization across ecological gradients. Given the deterministic framework of vegetation composition and structure (Murdoch et al. 1972; Brown et al. 1992; Niemela et al. 1996) and long evolutionary interactions between leafhoppers and plants, the communities might be highly integrated (Maczey et al. 2005, Agrawal et al. 2006). However, there have been few tests of AH community organization from across a broad, relatively intact ecosystem (e.g., Eyre et al. 2001) and, to our knowledge, none utilizing closely correlated sample data.

Although grassland habitats have been declining globally due to conversion to cropland, overgrazing, and woody encroachment (Gibson 2009), extensive arid and montane grasslands remain in Central Asia (McCloud 1974), particularly the Kyrgyz Republic (Nikol'skii 1994; Borchardt et al. 2011; Taft et al. 2011). The Tien Shan mountain range is a major component of the physiography of this region and a variety of habitats from desert grasslands to meadow steppe and alpine areas are present. In this study, we examine the interaction of AH and vegetation community structure along ecological gradients in the central Tien Shan Mountains as an exploration of primary assembly rules. We predict using standardized AH–vegetation sample data from throughout a biogeographic region evidence of concordance in community structure between AH and vegetation. Because previously we had identified a mid-elevational peak of plant species diversity (Taft et al. 2011), we predict a similar pattern for leafhoppers. We further explore whether variation in AH species assemblages across ecological gradients reflects a predominance of abiotic (environmental) or biotic (vegetation structure) factors and how these change with ecological scale. Accordingly, we address these specific research questions:

Question 1 What are the overall dominant AH species in grassland habitats of the central Tien Shan and how do zoogeographic affiliations compare with phytogeography?

Question 2 How do the AH frequency distribution and species accumulation profiles compare with plants?

Question 3 Does the plant community classification provide a valid framework for distinguishing AH species assemblages?

Question 4 Do known AH host preferences correlate with vegetation structure?

Question 5 How do AH species association, diversity, and abundance patterns vary across ecological gradients?

Question 6 What are the most prominent biotic and abiotic factors in structuring AH species assemblages across ecological gradients? By estimating the proportion of explained variance from samples recorded across broad ecological gradients, we hope to facilitate future predictions, particularly with regard to effects of climate change.

Methods

Study area

Joint entomological and botanical surveys were conducted at 118 predominantly grassland sample sites in the Kyrgyz Republic from 1998 to 2000. The Kyrgyz Republic (Kyrgyzstan) is a Central Asian country (199,900 km²) located

between China, Kazakhstan, Uzbekistan, and Tajikistan. Auchenorrhyncha botanical study sites were distributed throughout the country (Fig. 1) except a prohibited sector in the southwest. Vacuum and sweep-net surveys identified 390 species of Auchenorrhyncha (Novikov et al. 2006), and collections were made of 1005 plant species. Quantitative AH and vegetation sample data were recorded at a subset of 42 of these sites along identical transects ranging in elevation from 675 m to 3530 m above sea level. Sample dates were during mid-August to early September (1998), June (1999), and July (2000). Geographic coordinates and elevation for each study site are available in Online Resource 1.

Vegetation sampling

Species composition was recorded using usually 20 quadrats (0.5-m²) stratified across a 10-m wide and 100-m long (1000-m²) sampling grid with quadrats placed at 5-m intervals offset at random distances (1–5 m) on alternating sides of each transect (Taft et al. 2011). Location and orientation of each sampling transect were determined randomly in representative habitats for each site avoiding areas with severe anthropogenic disturbance. All vascular plants rooted within quadrats were identified and percent cover for each species and percent bare ground were estimated with modified Daubenmire cover classes. Voucher specimens for most recorded species have been placed in the herbarium of the Illinois Natural History Survey (ILLS). Species abundance is based on importance values (IV) calculated as the sum of relative frequency and relative cover. Vegetation structure was based on percent cover, percent bare ground, species density, species

diversity, and functional group density. Measuring vegetation height (vertical structure) initially was attempted at study sites, but ultimately abandoned due to a high degree of within-site heterogeneity and time limitations.

Auchenorrhyncha sampling

Insects were collected using both a leaf-blower vacuum sampler (~5 min of vacuuming per sample; Wallner et al. 2013a) and by sweep-net sampling (200 sweeps with a standard 38-cm diameter sweep net per sample) along each vegetation transect generally during the mid-day period. Auchenorrhyncha later were sorted to species and pinned or stored in 70% ETOH and vouchers were deposited in the insect collections of the Illinois Natural History Survey. Species abundance is based on counts of individuals. Auchenorrhyncha geographical patterns and host preference were determined based on distributional data available in the literature and following generally accepted biogeographic divisions for the Palearctic region (Nast 1972).

Habitat classification and description

Cluster analysis was used to produce a classification of sites from vegetation sample data (Taft et al. 2011). Following the classification of Vykhotsev (1976), seven vegetation types ranging from desert grassland to meadow steppe were identified from the sample data, ordered primarily along a gradient of elevation and mean annual temperature. Sites were divided into two main branches from the root of the cluster dendrogram. One branch comprised three montane communities (2457-m mean

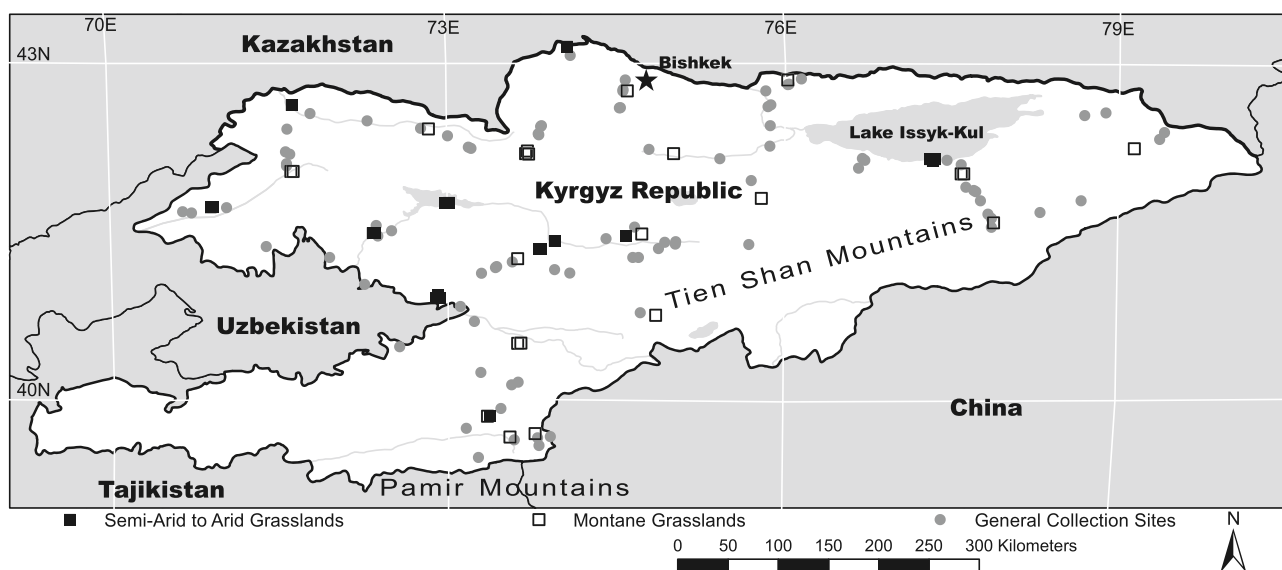


Fig. 1 Locations for quantitative and general entomological and botanical collections in grassland habitats of the Kyrgyz Republic

elevation): Class 1—montane steppe, Class 2—meadow steppe, and Class 3—montane meadow. The other branch was comprised of four arid to semi-arid communities (1304 m mean elevation): Class 4—sub-shrub semi-desert/montane semi-savanna, Class 5—montane semi-savanna/montane steppe, Class 6—sub-shrub semi-desert/semi-savanna (with elements of montane steppe), and Class 7—desert grassland. Montane grasslands ($n = 23$) were distinguished from arid grasslands ($n = 19$) by dominance of the C_3 grass *Festuca valesiaca*, numerous forbs, other C_3 grasses, and the absence of C_4 grasses. The arid grasslands were distinguished by the presence of C_4 grasses, woody species (mostly subshrubs of the genus *Artemisia*), short-lived species (annuals, biennials), and the near absence of *Festuca valesiaca*. Transitions from arid to montane grasslands generally occurred between 1500- and 1900-m elevation and where mean annual temperatures are less than 6 °C. Several significant indicator plant species were identified for each vegetation type (Taft et al. 2011).

The greatest plant species richness and percent cover were found in meadow steppe habitat at intermediate elevations between 1800 and 2600 m; however, species density (in 0.5/m² quadrats) varied widely across the elevation gradient with only a weak hump-shaped pattern best fit with a third-order polynomial trend line. A plurality of species (46%) was Central Asian endemics followed by species primarily with origins in western Siberia, the Caucasus, and Eastern Europe with more minor contributions from species with centers of distribution in eastern Siberia and far eastern Asia (Taft et al. 2011).

Land use throughout study areas included grazing (open range) and mowing (mostly by scythe), practices known to influence arthropod assemblages (Morris 1973; Kruess and Tschardtke 2002; Biedermann et al. 2005). Generally, grazers in arid and semi-arid habitats included goats and cattle while horses and sheep were the predominant grazers in montane grasslands. It is likely that to varying degrees, habitats at all study sites were affected by these land uses. In some cases, grazing animals were present at the time of study. However, past land administration in the Kyrgyz Republic has not been well organized (UNECE 2010) and we were unable to determine with any precision the intensity or duration of grazing or other land-use practices at each study site.

Data analysis

Analyses were conducted using Primer Version 7 (Clarke and Gorley 2015), PC-ORD Version 5.31 (McCune and Mefford 2006), and SPSS Version 23.1 (IBM 2015).

Question 1 Overall dominant AH species were determined by calculating an importance value based on relative frequency and relative abundance.

Question 2 Frequency distribution and species accumulation curves from AH and plant species sample data were compared with Kolmogorov–Smirnov two-sample tests. Mean number of occurrences between AH and plant species were compared with two-sample t-tests.

Question 3 A classification of sites based on a cluster analysis of vegetation sample data provided the foundation for determining how the AH species assemblages correspond with vegetation classes. Cluster analysis was based on the clustering algorithm of Wishart (1969) and Post and Sheperd (1974). Flexible sorting with β set at -0.25 was used for its optimal grouping characteristics (Lance and Williams 1967) to construct a hierarchical dendrogram from Sørensen distance measures. The dendrogram was pruned based on results from indicator species analysis (Dufrene and Legendre 1997) and recommendations by McCune and Grace (2002). Values from indicator species analysis also were used to identify taxa modal to particular community types with significance determined from Monte Carlo randomization tests (4999 iterations). Differences in AH species assemblages formed by vegetation classes were examined with one-way analysis of similarity (ANOSIM) to test the null hypothesis of no difference among unordered groups (Clarke and Green 1988). The ANOSIM global test statistic R is based on the difference of average similarities between and among groups so that R varies from 0 (no differences) to 1 (complete compositional differences) with significance determined from permutations of all possible comparisons (Clarke and Gorley 2015). In addition to global tests, pairwise test results explore differences between classes.

Question 4 The association between AH host preference and vegetation structure was examined with indirect gradient analysis using nonmetric multidimensional scaling (nMDS) (Kruskal and Wish 1978).

Question 5 Variation in AH species assemblages among sites was also examined with nMDS. We then searched for correlations between the ordinations and arrangements of host preference and AH species abundance, richness, diversity, dominance, evenness, and AQI [an index of AH community integrity (Wallner et al. 2013a); we utilized the quantitative modification] to examine patterns corresponding to the axes. For both nMDS ordinations, we used Bray–Curtis distance measure and a random starting configuration; results from 500 random starts of nMDS were examined in two to six dimensions. nMDS was used for its independence from species response models and optimal graphical representation of community relationships (Clarke 1993). Differences in beta diversity among AH and plant species assemblages, based on species presence–absence, were tested using

within-group dispersion and the distance-based test (Sørensen similarity) for homogeneity of multivariate dispersions (PERMDISP) (Anderson et al. 2006).

Question 6 Variance in the AH species assemblages associated with predictor variables was examined with distance-based linear models (DistLM) which examine the fit of individual parameters with marginal tests. Stepwise sequential tests, the result of forward selection and backward elimination at each step, were utilized for determining the best combination of predictors. Distance-based redundancy analysis (dbRDA) was used for ordination and the graphical depiction of the fitted DistLM models (Legendre and Anderson 1999; McArdle and Anderson 2001). Predictor variables included 14 related to structure and diversity patterns in the vegetation:

% Cover	% IV Woody
% Bare Ground	Plant Functional Group Density
% IV Annual/Biennial Forb	Species Density [spp. #/quadrat (0.5-m ²)]
% IV Perennial Forb	Species Richness (species #/transect)
% IV C ₃ grass	Evenness
% IV C ₄ grass	Diversity (Shannon–Wiener index)
% IV Sedge	Dominance (Simpson's index)

Six predictor variables were based on environmental/geospatial variables: Mean Annual (M. A.) Temperature, Elevation, M. A. Precipitation, Latitude, Longitude, Day # (since 1 January, a proxy for season; sample dates extended from mid-June to mid-September). Further details on vegetation sampling and source data for environmental variables can be found in Taft et al. (2011).

These predictor variables were examined to assess whether habitat structure or environment explain the most variance in AH species assemblages. The direct interaction between patterns of leafhopper and plant species richness and diversity were examined with the coefficient of determination (R^2).

Data preparation

Multivariate analyses of community data were based a Bray–Curtis resemblance matrix and square-root transformed species abundance data for Auchenorrhyncha to limit the role of dominant species in similarity calculations. Environmental and habitat data were prepared for analysis by exploring residuals for visible nonlinear trends and the Ryan–Joiner test for normality (Ryan and Joiner 1976). Most parameters were normally distributed; parameters

with evident skewed patterns were modified with the Box–Cox or Johnson transformations using Minitab 17 (Minitab, Inc., State College, PA). Box–Cox is a power transformation algorithm for positive data (Box and Cox 1964), while the Johnson algorithm utilizes a family of statistical functions for transforming frequency curves (Johnson 1949). However, data were analyzed using both transformed and untransformed values with only minor differences in outcome, noted in Results. Since the minor difference in outcome did not alter interpretation, the untransformed values were used for direct gradient analysis. Predictor variables were examined for multi-collinearity. Highly correlated variables ($r \geq 0.9$ or $r \leq -0.9$) were reduced to one variable (Elevation–M. A. Temperature, Diversity [H']-Dominance, Diversity–Species Richness, % Cover–% Bare Ground). Environmental data and habitat variables based on vegetation structure were normalized for comparison by subtracting the mean for each variable and dividing by the standard deviation. Species abundance data were converted to presence–absence for determining beta diversity.

Results

Auchenorrhyncha community composition, structure, and zoogeography

Total AH species recorded in 42 transects sampled throughout the Kyrgyz Republic was 138, predominately Cicadellidae [99 species (71.7%)] and Delphacidae [16 species (11.6%)]. The remaining species represented seven other families [Dictyopharidae (6), Issidae (4), Tettigometridae (4), Aphrophoridae (3), Cixiidae (3), Calicelidae (2), Tropiduchidae (1)]. Mean species richness was 9.62 ± 0.83 (SE) and total count of individuals averaged 98.3 ± 15.9 . A total of 4129 AH individuals were recorded in the transect samples. Overall dominant species were *Diplocolenus frauenfeldi*, *Eohardya fraudulenta*, *Emeljanovianus medius*, *Handianus imperator*, *Nealiturus haematoceps* (group), *Psammotettix monticulinus*, *Hysteropterum montanum*, *Psammotettix comitans*, *Psammotettix striatus* (group), and *Psammotettix dubovskii*. All are Cicadellidae except *H. montanum* (Issidae). These top 10 ranking species account for 40.7% of the total importance (IV) among species.

Most species were infrequent. Nearly 45% of AH species were recorded from a single transect and less than 5% had ≥ 10 occurrences (Fig. 2a). The frequency distribution of species occurrences among AH and plant species assemblages were similar (Kolmogorov–Smirnov $Z = 0.632$, $P = 0.82$). Mean occurrences among transects were slightly greater among AH species (2.88 ± 0.1)

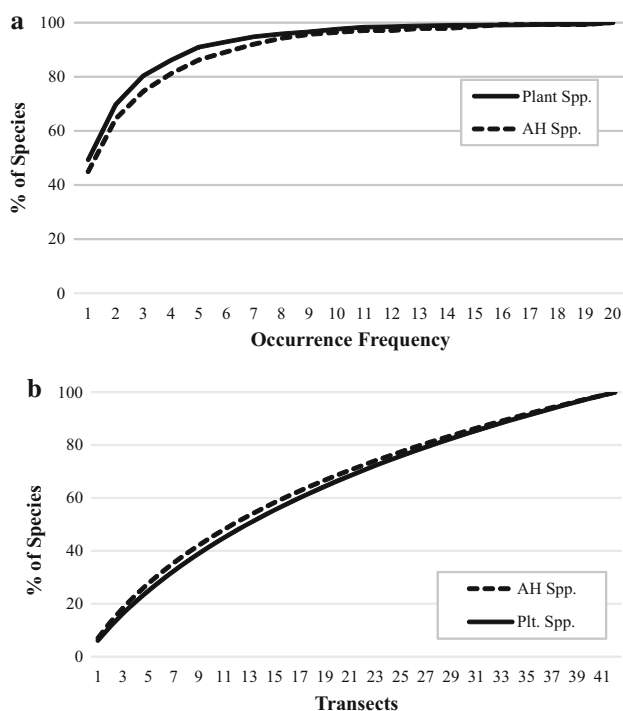


Fig. 2 Frequency distributions (a) and proportionate species accumulation curves (b) comparing results from leafhopper and plant species sample data along identical transects in grassland habitats of the Central Tien Shan

compared to plants (2.57 ± 0.1); however, the differences were not significant ($t = 1.08$, $df = 187$, $P = 0.28$). Although no asymptote is reached following 42 sampling transects, the proportionate species accumulation curves between AH and plant species (Fig. 2b) were statistically identical (Kolmogorov–Smirnov $Z = 0.231$, $P = 1.0$).

Based on zoogeographic affiliations, AH communities recorded from transects were dominated in terms of taxa number and total abundance by Western Palearctic and, secondarily, Central Asian species (Fig. 3). Western Palearctic species total 37% and comprise 51% of total abundance; Central Asian taxa totaled 27% of both species

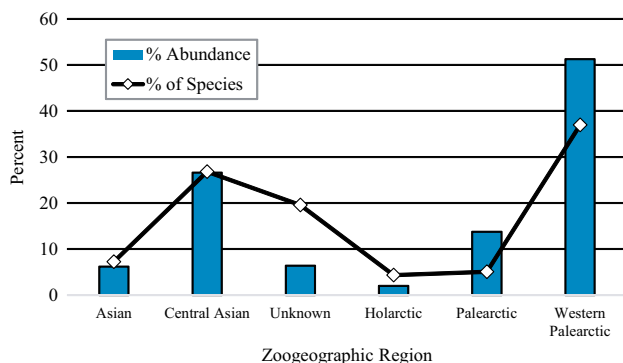


Fig. 3 Zoogeographic affinities for leafhopper species recorded from 42 sample transects in grassland habitats of the Central Tien Shan

number and abundance. Species with uncertain distributions (taxa unidentified to species) rank third in number but have minor total abundance. Species with Palearctic, Asian, and Holarctic affiliations had overall relatively minor representation.

Community classification, indicator species, and host preference

AH species assemblages defined by vegetation classes were significantly different (ANOSIM $R = 0.307$, $P = 0.0001$) with no randomized permutations (out of 9999) achieving the observed level of between-group differences. Out of 21 possible pairwise comparisons among classes, 13 were significantly different. However, four pairwise comparisons were intermixed more than expected by random chance. Most notably, the AH species assemblages in montane steppe (Veg. Class 1) were indistinguishable from AH assemblages in two arid grassland community classes: Montane semi-savanna (Class 5) and Sub-shrub semi-desert/semi-savanna (Class 6); both these arid grassland types included minor floristic elements from montane steppe communities. This lack of discrimination between montane steppe and more arid grassland classes is driven by a small set of dominant, widespread species [e.g., *Handianus imperator*, *Psammotettix striatus*, *P. dubovskii*, *Neoliturus haematoceps* (group), *Praganus hofferi*, and *Rhoananus hypochlorus* (Table 1)]. Of the 138 taxa, 47 were relatively common (≥ 10 individuals) in at least one vegetation type and 15 were identified as significant indicators of vegetation classes, seven among the montane communities and eight among the arid grassland classes including the five listed above (Table 1).

Host preference for Auchenorrhyncha was predominantly Poaceae in both total species number and abundance (Fig. 4). AH specializing on Poaceae and Cyperaceae were in greatest number and abundance among the montane (C_3) grasslands, and polyphagous species and forb-feeding specialists were more prevalent among arid grasslands; however, only grass and sedge specialists were significantly correlated ($P < 0.05$) with nMDS axes (Fig. 5).

The general pattern of dominance of AH species richness and abundance with Western Palearctic and secondarily Central Asian distributions holds for montane and arid grassland types; however, species with widespread Asian distributions were relatively more abundant in the arid grassland types (17.9% of total abundance compared to 1.3% in montane grasslands). Species with Palearctic and Holarctic distributions were minor components with the exception of the Meadow Steppe community where widespread Palearctic species ranked third with 22% of total abundance.

Table 1 Dominant (bold) and significant indicator species (italics) of Auchenorrhynchos Hemiptera from seven vegetation classes identified by cluster analysis from 42 sampling transects in grasslands throughout the Kyrgyz Republic

	CLASS 1		CLASS 2		CLASS 3		CLASS 4		CLASS 5		CLASS 6		CLASS 7	
	#	IS	#	IS	#	IS	#	IS	#	IS	#	IS	#	IS
<i>Diplocolenus frauenfeldi</i> (Fieb.)	14		<i>421</i>	<i>60.1</i>	0		0		0		5		0	
<i>Eohardya fraudulenta</i> (Horv.)	166		172		0		0		8		1		0	
<i>Emeljanovianus medius</i> (M.R.)	6		169		162		0		1		1		0	
<i>Hysteropterum montanum</i> (Beck.)	104		68		0		0		6		15		0	
<i>Handianus imperator</i> Dlab.	26		15		0		2		<i>92</i>	<i>48.6</i>	50		0	
<i>Psammettix comitans</i> Em.	0		4		0		2		<i>118</i>	<i>46.3</i>	38		2	
<i>Psammettix striatus</i> (group)	20		9		27		9		0		39		0	
<i>Psammettix dubovskii</i> Vilb.	23		46		13		0		1		15		0	
<i>Nealiturus haematoceps</i> (group)	18		0		0		4		33		35		4	
<i>Praganus hofferi</i> (Dlab.)	42		0		0		1		29		11		0	
<i>Diplocolenus abdominalis</i> (F.)	25		35		20		0		0		0		0	
<i>Anaceratagallia venosa</i> (Fourcr.)	7		4		0		0		25		22		0	
<i>Emeljanovianus pratensis</i> Em.	0		26*		<i>23</i>	<i>51.0</i>	0		0		0		0	
<i>Rhoananus hypochlorus</i> (Fieb.)	20		0		0		0		0		24		0	
<i>Arocephalus languidus</i> (Flor.)	0		26		13		0		0		0		0	
<i>Hardya turanica</i> Zachv.	67		0		0		1		0		4		0	
<i>Tettigometra vitellina</i> (F.)	18		0		0		0		0		4		0	
<i>Stenometiellus dzhungaricus</i> Mit.	13		2		0		0		0		0		0	
<i>Metropis mayri</i> Fieb.	13		0		0		0		0		0		0	
<i>Cicadula frontalis</i> (H.-S.)	11		0		0		0		0		0		0	
<i>Lepyronia coleoprata</i> (L.)	10		1		0		2		0		1		0	
<i>Psammettix monticulinus</i> Em.	1		230		0		0		0		0		0	
<i>Mongolojassus tianshanicus</i> Mit.	0		110		0		0		0		0		0	
<i>Scleroracus transversus</i> (Fall.)	0		72		4		0		0		0		0	
<i>Pinumius areatus</i> (Stal.)	0		57		0		0		0		0		0	
<i>Tiaratus caricis</i> Em.	0		50		0		0		0		0		0	
<i>Macropsidius abrotani</i> Em.	0		44		0		0		0		0		0	
<i>Henschia collina</i> (Boh.)	2		36		4		0		0		3		0	
<i>Clorionidea bromi</i> Em.	0		34		0		0		0		0		0	
<i>Ribautodelphax</i> sp.	0		34		0		0		0		0		0	
<i>Dicranotropis</i> sp.	0		23		0		0		0		0		0	
<i>Psammettix provincialis</i> (Rib.)	0		19		0		0		0		0		0	
<i>Evacanthus asiaticus</i> Osh.	5		17		0		0		0		0		0	
<i>Doratura concors</i> Horv.	5		16		0		0		1		0		0	
<i>Aphrodes bicincta</i> (Sch.)	0		16		0		0		0		0		0	
<i>Metropis</i> sp.	0		15		0		0		0		0		0	
<i>Agallia</i> sp.	2		13		0		0		0		1		1	
<i>Aphrodes</i> sp.	0		7	<i>36.4</i>	0		0		0		0		0	
<i>Doratura stylata</i> (Boh.)	0		7		5	<i>48.2</i>	0		0		0		0	
<i>Psammettix confinis</i> (Dahl.)	8		0		<i>84</i>	<i>96.9</i>	0		0		0		0	
<i>Psammettix</i> sp.	0		2		<i>63</i>	<i>95.2</i>	1		0		2		1	
<i>Psammettix alienus</i> (Dhlb.)	0		0		24		0		0		0		0	
<i>Balclutha</i> sp.	2		4		<i>10</i>	<i>51.1</i>	0		0		3		0	
<i>Trypetimorpha fenestrata</i> A. Costa	0		1		0		76		0		0			
<i>Aconurella quadrum</i> (H.-S.)	0		0		0		10		1		0		0	
<i>Parapilaenus notatus</i> (M.R.)	0		0		0		8	<i>75.0</i>	0		0		0	

Table 1 continued

	CLASS 1		CLASS 2		CLASS 3		CLASS 4		CLASS 5		CLASS 6		CLASS 7	
	#	IS	#	IS	#	IS	#	IS	#	IS	#	IS	#	IS
<i>Laburrus handlirschi</i> (Mats.)	0		0		0		5	50.0	0		0		0	
<i>Batracomorphus irroratus</i> Lew.	2		2		0		1		125		1		0	
<i>Handianus procerus</i> (H.-S.)	1		0		0		0		11	38.1	0			
<i>Stenometopiellus oxianus</i> Diab.	2		0		0		0		8	35.1	0			
<i>Euscelis seriphidii</i> Em.	0		0		0		0		0		21			
<i>Henschia acuta</i> (Low)	0		0		0		0		0		0		24	66.7
<i>Pseudophlepsius binotatus</i> (Sign.)	0		0		0		0		0		0		6	100.0
Sum	746		1877		473		147		493		353		40	
% of total	79.1		94.0		92.8		58.5		87.8		76.5		60.0	
Mean spp. richness	11.0		10.7		10.3		7.8		9.0		9.7		4.0	

Dominant species have >9 count for each vegetation class. Species >9 individuals in more than one vegetation class are listed at top, sorted in descending order of sum count. Subsequent species are remaining dominants and significant indicator species for each vegetation class

IS significant indicator species identified with indicator species analysis

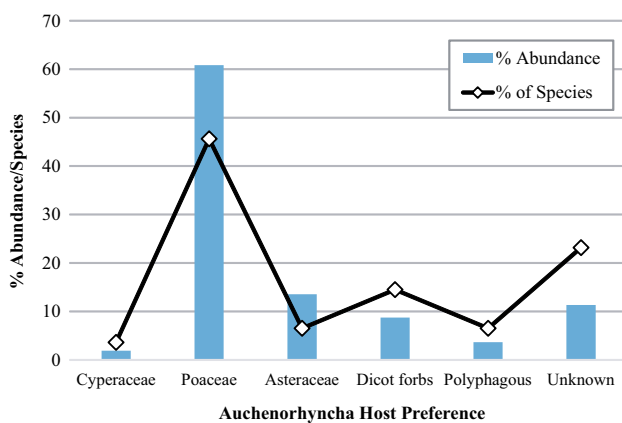


Fig. 4 Percent total abundance and species number according to auchenorrhynchan host preference recorded among sample transects in grassland habitats of the central Tien Shan

Auchenorrhyncha species association, diversity, and abundance patterns

Results from nMDS examining AH species associations, abundance, species richness, and diversity indicate that a three-dimension solution provided the best configuration (stress value 0.13). Generally, montane (vegetation classes 1–3) and arid grassland sites (vegetation classes 4–7) are divided at the midpoint along the first MDS axis; however, corresponding to the ANOSIM results, the MDS 1 × MDS 3 projection reveals a few assemblages from sites classified as montane steppe associating more closely with arid grassland AH species assemblages (Fig. 6). AH species richness and abundance are positively associated with the

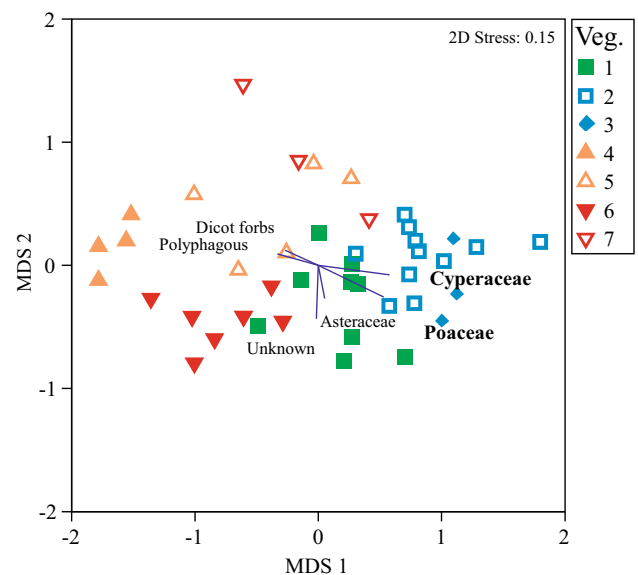


Fig. 5 Nonmetric multidimensional scaling ordination diagram illustrating vectors for auchenorrhynchan Hemiptera (AH) host preference in plant functional group ordination space. Only AH specialists on Cyperaceae ($r = 0.36$) and Poaceae ($r = 0.33$) were significantly associated ($P = 0.01$ and 0.02 , respectively) with ordination axes, positively correlated with the first axis and associated montane steppe, meadow steppe, and montane meadow communities. Plant functional group data were square-root transformed and the resemblance matrix is based on Bray–Curtis similarity. Key to symbols: Veg. Class 1 (filled square) = montane steppe, Veg. Class 2 (open square) = meadow steppe, Veg. Class 3 (filled diamond) = montane meadow, Veg. Class 4 (filled triangle) = sub-shrub semi-desert/semi-savanna, Veg. Class 5 (open triangle) = semi-savanna/montane steppe, Veg. Class 6 (inverted filled triangle) = sub-shrub semi-desert/semi-savanna, Veg. Class 7 (inverted open triangle) = desert grassland

first MDS axis (Table 2) and correspondingly with most montane grassland communities. AQI, an index of leafhopper species integrity, is positively associated with the first MDS axis.

Beta diversity among AH assemblages formed by the vegetation classes were significantly different (mean dispersion 46.5, $F = 8.7$, $P = 0.0004$). Beta diversity was greater in the montane grassland communities ($n = 23$, mean dispersion 61.8) compared to the more arid grasslands ($n = 19$, mean dispersion 54.4), and the difference was significant ($F = 11.3$, $P = 0.002$). Mean dispersion among plant species assemblages was similar overall to AH communities (45.97, $F = 11.0$, $P = 0.0002$); plant beta diversity in montane communities (mean dispersion 59.95) also was greater than arid grasslands (mean dispersion 57.5), and the difference was significant ($F = 5.2$, $P = 0.036$). Among montane grasslands, beta diversity was greater among AH species assemblages (61.8) compared to plant assemblages (59.95); however, among arid grasslands, beta diversity was greater among plant species assemblages (57.5) compared to arid AH species assemblages (54.4).

Auchenorrhyncha–habitat and environment relations

AH species richness and abundance were positively correlated with plant species density, diversity, and percent cover (Fig. 7a–c, e). Analysis of residuals from the correlation between leafhopper and plant species richness revealed that sites among vegetation classes were divided equally above and below the mean with the exception of Class 7 (Desert Grassland) where AH richness consistently was less than

Table 2 Pearson correlation coefficients comparing Auchenorrhynchos Hemiptera (AH) community parameters and environmental factors with nonmetric multidimensional scaling axes.

	MDS1	MDS2	MDS3
AH sum count	0.499	0.249	0.032
AH spp. richness	0.339	0.053	0.059
AH evenness	−0.080	−0.100	−0.138
AH diversity	0.081	−0.057	−0.074
AH dominance	−0.035	0.036	0.142
AQI	0.360	0.140	0.148

Values in bold are significant ($P < 0.05$)

expected based on plant species density. AH species richness formed a peak at intermediate elevations between 1600 and 3100 m (Fig. 7d). Two species-rich exceptions at lower elevations were from early-season (June) samples in both arid and montane grassland sites. AH species richness declined with increasing percent bare ground (Fig. 7f).

Marginal test results from distance-based linear models (DistLM) of the independent interaction between the AH species assemblages and habitat structure and environmental factors indicate significant interactions with 15 of the 16 variables with Latitude the lone exception (Table 3). Best fit variables determined with stepwise sequential tests indicate that Elevation, Plant Species Density, Mean Annual Precipitation, Season (Day #), Evenness, % Cover, and % Woody explain significant portions of the variance in the AH species assemblage (Table 3). Three graminoid functional groups are each nearly significant (sedge $P = 0.06$, C_3 grass $P = 0.08$, and C_4 grass $P = 0.07$); when combined, % Graminoid cover is marginally significant ($P = 0.056$). Of the significant factors ($P < 0.05$), environmental factors account for 53.3% of the sum explained variance and habitat factors explain 46.7%. Adding Graminoid to the model (and removing sedge, C_3 grass, and C_4 grass), habitat factors explain 50.9% of the variance. There remains much unaccounted for variance in the AH species assemblage: based on adjusted R^2 , only 16.6% of the total variation is explained by the measured factors in the first two dbRDA axes (Fig. 8) and only 22.4% of the variance [adjusted R^2 ($R^2 = 0.47$)] is explained by all fitted variables in the model (Table 3).

Partitioning arid and montane grasslands reveals that habitat explains more variance than environment for both major grassland types (57% to 42% and 61% to 39% in arid and montane sites, respectively) but the principle factors differ (Table 4). In arid grasslands, principle habitat factors were Plant Species Density, Plant Functional Group Density, and % Cover Perennial Forbs, while M. A. Precipitation and Season are predominant environmental variables. In montane grasslands, principle habitat factors were % Cover of Perennial Forbs, % Cover of Woody species, % Cover of Sedges, Plant Species Density, and Species

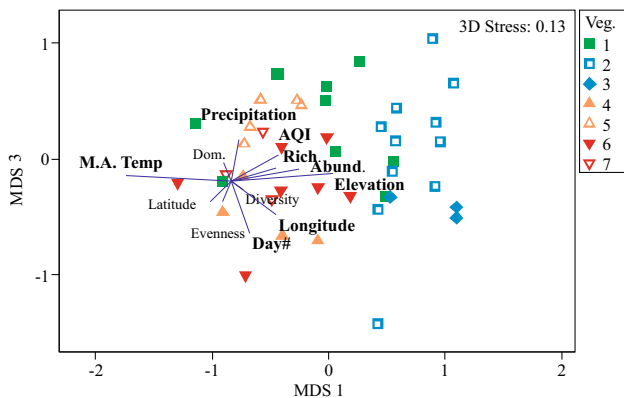


Fig. 6 Nonmetric multidimensional scaling ordination diagram illustrating vectors for auchenorrhynchan Hemiptera (AH) species richness, diversity, abundance, and AQI (auchenorrhynchan quality index) in AH ordination space. AH species data were square-root transformed and the resemblance matrix is based on Bray–Curtis similarity. Veg vegetation classes 1–7 (see caption Fig. 5 for key to symbols); Classes 1–3 are montane grasslands and 4–7 are arid grasslands

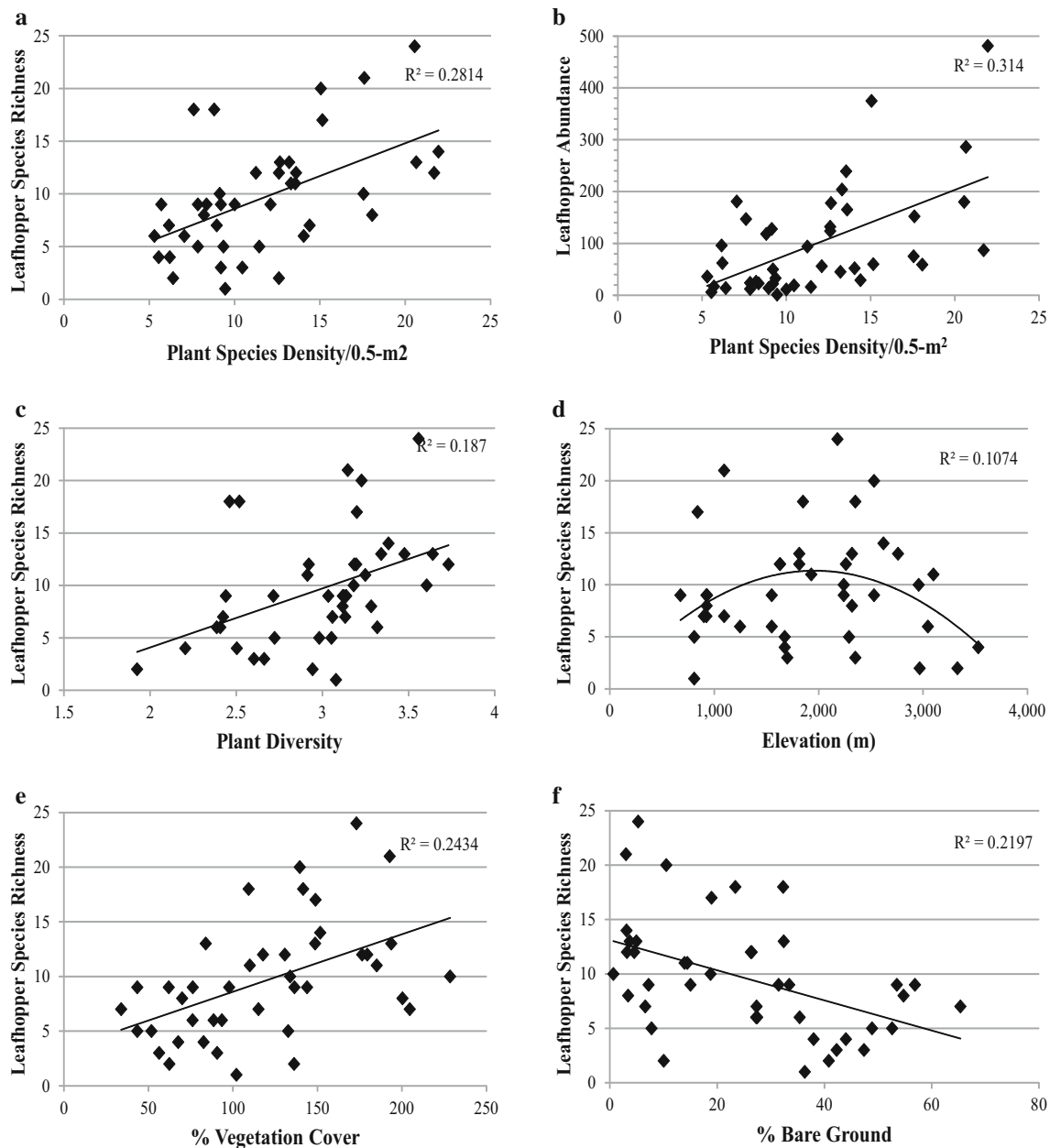


Fig. 7 Correlations of auchenorrhynchan Hemiptera species richness and abundance with prominent plant community and environmental parameters

Diversity, while Elevation, Longitude, and Season were predominant environmental factors.

Discussion

Representativeness of samples

Auchenorrhyncha species richness recorded in 42 transects was 35% of the total recorded in 618 general samples from all 118 study sites. Similar to general survey results

(Novikov et al. 2006), most species were Cicadellidae [72% (63.5% in general surveys)] followed by Delphacidae [12% (16.6% in general surveys)]. Some discrepancy is expected because general sampling included sweeping trees and shrubs (which would have yielded additional leafhoppers as well as non-delphacid planthoppers, e.g., dictyopharids and cixiids) and wetlands, which have proportionately more delphacids.

Zoogeographic affiliation of AH species from transect samples was similar to the pattern from general samples. However, Central Asian taxa were more dominant in the

Table 3 Marginal and stepwise sequential test results from distance-based linear models of the interaction between auchenorrhychous Hemiptera and habitat structure (from vegetation sample data) and environmental factors.

Variable class	Variable	SS (trace)	Pseudo- <i>F</i>	Prob.	
Habitat structure—diversity	Plt Spp. Density	10,995.0	2.69	0.0001	
	Plt Evenness	10,386.0	2.54	0.0002	
	Plt Diversity	7860.7	1.89	0.0027	
Habitat structure—Physiog.	% Veg Cover	9659.6	2.35	0.0002	
	% IV A/B Forb	9801.0	2.38	0.0002	
	% IV P Forb	11,237.0	2.76	0.0002	
	% IV C ₃ Grass	7773.5	1.87	0.0041	
	% IV C ₄ Grass	9892.9	2.41	0.0001	
	% IV Sedge	6049.4	1.44	0.0474	
	% IV Woody	12,194.0	3.01	0.0001	
	Plt FG Density	9213.3	2.23	0.0003	
Environment	Elevation	14,426.0	3.61	0.0001	
	M.A. Precipitation	8020.9	1.93	0.0031	
	Latitude	4409.1	1.04	0.3927	
	Longitude	9124.2	2.21	0.0008	
	Day # (since 1 Jan)	7384.7	1.77	0.0064	
Sequential tests					
	Variable	Adj. <i>R</i> ²	Prob.	Prop. <i>R</i> ²	Cum. <i>R</i> ²
Environment	+Elevation	0.060	0.0001	0.083	0.083
Habitat structure—diversity	+Plt. Spp. Density	0.087	0.0001	0.049	0.132
Environment	+M.A. Precipitation	0.113	0.0001	0.046	0.178
Environment	+Day # (since 1 Jan)	0.135	0.0008	0.041	0.220
Habitat structure—diversity	+Evenness	0.166	0.0058	0.034	0.288
Habitat structure—Physiog.	+% Cover	0.150	0.0079	0.034	0.254
Habitat structure—Physiog.	+% IV Woody	0.180	0.0136	0.032	0.320
Habitat structure—Physiog.	+% IV Sedge	0.189	0.0605	0.027	0.348
Habitat structure—Physiog.	+% IV C ₄ Grass	0.208	0.0684	0.027	0.401
Habitat structure—Physiog.	+% IV C ₃ Grass	0.198	0.0847	0.026	0.374
Environment	+Latitude	0.221	0.1522	0.024	0.449
Habitat structure—diversity	+FG Density	0.214	0.1831	0.024	0.425
Environment	+Longitude	0.224	0.2883	0.021	0.470

Values in bold are significant ($P < 0.05$)

Plt. plant, *Physiog.* physiognomy, *IV* importance value, *A/B* annual/biennial, *P* perennial, *FG* functional group, *M.A.* mean annual

general survey results with 43.6% of species compared to 26.8% in the transect sample data. Western Palearctic taxa were 35.5 and 37% of species in the general and transect samples, respectively. Unknown taxa comprised nearly 20% of species in the transect samples. If these are Central Asian species, as suggested for most of the unknown taxa in the general surveys (Novikov et al. 2006), the proportion of zoogeographic affinities would very closely match the general survey data. These results suggest that combined sweep-net and vacuum sampling in exemplary habitat patches captured a representative sample of the local AH species assemblages.

Phylogeographic affiliations were similar to AH species. Species with centers of distribution in Western Siberia

(similar to the Western Palearctic zoogeographic region) were dominant in terms of species number followed by Central Asian species; however, plant species abundance had greater dominance of Central Asian species (Taft et al. 2011) while Central Asian AH species ranked second in overall abundance.

Community classification

The vegetation classification provides a realistic framework for examining AH species assemblages, while AH assemblages provide insights for examining the independent response of AH species to transitional communities. Other AH surveys and ground beetle communities also

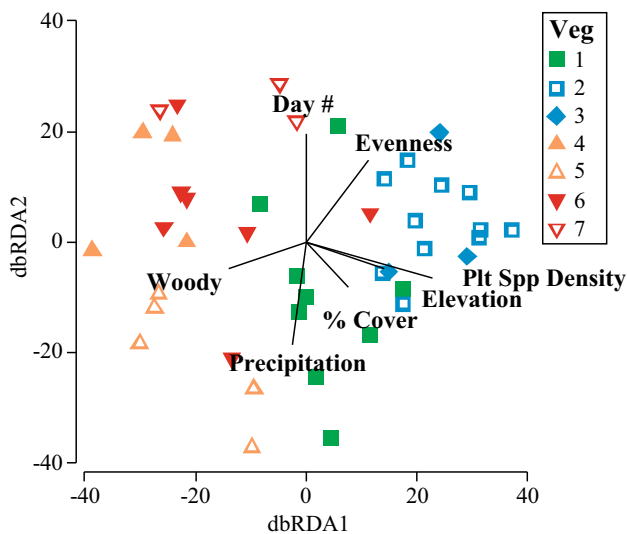


Fig. 8 dbRDA ordination from the fitted distance-based linear model of achenorrhynchan Hemiptera species abundance with habitat and environmental variables. Total explained variation in the fitted model in two axes is 51.8%; cumulative explained out of total variance in first two axes is 16.6%. Veg vegetation classes 1–7 (see caption Fig. 5 for key to symbols). Classes 1–3 are montane grassland and 4–7 are arid grassland

have been found to have a strong link with vegetation communities (Novotny 1990; McCoy 1990; Yanahan and Taylor 2014). AH species assemblages from arid and montane grasslands mostly form discrete clusters, similar to plants, with some mixing at the ecotone between the groups (Fig. 6). Assemblages of AH species from arid grasslands associating with montane steppe might be expected with an upward trend of species along elevational gradients with climate change, if the synchrony between insects and plants is altered by differences in the pace of change (e.g., Frei et al. 2014; Rasmann et al. 2014a). This pattern of mixing at this particular transition was surprising due to fundamental differences in floristic composition between arid and montane grasslands. The AH species that contribute to this pattern include widespread but primarily flightless Poaceae feeders. Our expectation was that if such a pattern was detected, the ecological filter at this transition zone would select for primarily macropterous rather than brachypterous species. A projected increase of *M. A.* temperature of 2 °C by mid-century is expected to shift altitudinal gradients in Scotland by 300 m (Whittaker and Tribe 1996) which could result in more mixing and perhaps a greater role for ecological filters in limiting which AH species respond most effectively. However, the responses of herbivorous insects along elevational gradients, particularly to increasing temperature, is highly complex and influenced by such factors as life history, the ecophysiological tolerances of host plant and predator species, habitat patch size, as well as dispersal ability (Hodkinson

2005). Add to this variation in land use, such as grazing which can greatly influence AH species assemblages (Brown et al. 1992; Dennis et al. 1998, Biedermann et al. 2005), and the synchrony in classification (e.g., ANOSIM results) appears particularly remarkable.

AH species richness and habitat/environmental factors

The apparent integration between AH and plant species with these sample data suggests three possibilities: strong biotic interactions, a mutual response to abiotic factors, or some combination.

AH–plant community correlations

There are many parallels in the structure of AH and plant communities identified from our coordinated sample data that suggest a high level of integration. Both have similar mean number of site occurrences among species, nearly identical pattern of frequency distributions among species, identical proportionate species accumulation curves, and strong positive correlation between patterns of AH species richness and abundance and plant alpha diversity. We also found known host preferences of AH assemblages to correlate with patterns of vegetation structure. The positive correlation between plant and herbivore insect species diversity has been observed for a variety of insect groups including Hemiptera (Murdoch et al. 1972), Lepidoptera (Erhardt and Thomas 1991, Hawkins and Porter 2003, Janz et al. 2006), and total arthropods (Siemann et al. 1998). The correlation is expected given that greater plant diversity often can be associated with greater resources for herbivores, including increased heterogeneity in vegetation architecture and functional groups (Lawton 1983). However, covariance with environmental factors can confound the role of species diversity alone. The positive correlation of Lepidoptera and plant diversity in California was determined to be a result of autocorrelation with environmental factors (Hawkins and Porter 2003), but this could be a result of remote analysis of broad patterns instead of closely associated sample data. Contrasting grain size, or unit of inferential analysis, can contribute to different interpretations of species richness patterns (Rahbek 2005) and likely also strength of environmental interactions.

Mid-elevation peak

The mid-elevation peak of AH species richness observed from our standardized samples also parallels the pattern for plant species and concurs with many other biotic patterns (Lomolino 2001; Rahbek 2005). Causes of mid-elevation peaks of species richness have been attributed to a variety

Table 4 Partitioned results of stepwise sequential test results from distance-based linear models of the interaction between auchenorrhychous Hemiptera and habitat structure and environmental factors for arid and montane grasslands.

Sequential test results: arid grasslands ($n = 19$)				
Variable	Adj. R^2	P	Prop. R^2	Cum. R^2
Environmental				
+Mean Annual Precipitation	0.063	>0.001	0.115	0.115
+Day # (since 1 Jan)	0.191	0.058	0.070	0.371
Sum R^2			0.186	
% of total R^2			42%	
Habitat variable				
+Plt FG Density	0.119	0.002	0.101	0.217
+Plt. Spp. Density	0.161	0.009	0.084	0.301
+% IV P Forb	0.300	0.039	0.070	0.572
Sum R^2			0.255	
% of total R^2			57%	
Sequential test results: montane grasslands ($n = 23$)				
Variable	Adj. R^2	P	Prop. R^2	Cum. R^2
Environmental				
+Elevation	0.162	0.007	0.072	0.353
+Longitude	0.093	0.026	0.067	0.217
+Day # (since 1 Jan)	0.121	0.031	0.064	0.281
Sum R^2			0.203	
% of total R^2			39%	
Habitat				
+% IV P Forb	0.033	0.007	0.077	0.077
+% IV Woody	0.064	0.010	0.072	0.149
+Plt. Spp. Density	0.192	0.032	0.060	0.413
+Plt Diversity	0.252	0.037	0.056	0.524
+% IV Sedge	0.220	0.056	0.056	0.468
Sum R^2			0.321	
% of total R^2			61%	

Values in bold are significant ($P < 0.05$)

Only the significant (bold) or marginally significant factors are included

Plt. plant, *Physiog.* physiognomy, IV importance value, A/B annual/biennial, P perennial, FG functional group, M.A. mean annual

of factors including outcome of a mid-domain effect resulting from geographic dispersal limitations (Grytnes 2003), disturbances (McCoy 1990), nutritional resource availability for phytophagous insects (Janzen 1973), and sampling effects (Wolda 1987). The observed pattern suggests either of two general processes: the ends-are-bad or the middle-is-good (McCoy 1990), although the two are not necessarily exclusive. Following the middle-is-good model, optimal growing conditions at mid-altitudes might contribute to improved resources for insect herbivores. In grasslands of the central Tien Shan, vegetation cover, measured as the sum of each species, peaks at mid-elevations along with plant alpha diversity. Following the ends-are-bad model, limits on species migration at ecological edges (e.g., low or high elevations) can be expected to

produce mid-elevation peaks (Laurie and Silander 2002). Habitat fragmentation which was greater in lower elevations and natural limits on AH dispersal at high elevations could contribute to the outcome. Other factors could include differences in palatability along elevational gradients (Pellisier et al. 2012, Rasmann et al. 2014a) and variation in the magnitude of land-use. AQI was lower among arid grasslands compared to montane grasslands reflecting a greater proportion of species in arid habitats with life history traits characteristic of ruderal taxa, such as macropterous and polyphagous species (Wallner et al. 2013a). Regarding predictions of diet specialization along elevation gradients, our observations of greater polyphagy at lower altitudes contrast with the altitude niche breadth hypothesis (Rasmann et al. 2014b) which predicts

increased polyphagy and less specialization at higher altitudes.

Regarding sampling effects, our late-season samples (mid-August to early September), had lower diversity and abundance compared to earlier samples. Such a trend is expected since palatability of grasses for ectophagous insects decline with tissue maturation (Tscharntke and Greiler 1995). Also, due to limited access by springtime snow-covered passes, our samples were collected during the early to late summer (mid-June–September). We may have missed some univoltine species, particularly in lower, drier habitats, that are active as adults earlier in the growing season. More mesic habitats tend to occur at higher elevation in the Tien Shan, and the AH faunas of these sites tend to mature later in the growing season. Thus, our sampling strategy may have been more likely to document faunas of higher elevation sites more completely. If short-term sampling utilized in this study biased arid grasslands more than montane grasslands, this could have contributed to the mid-elevational peak in AH species richness, but it is unclear if the monotonic declines found in long-term tropical insects samples (Wolda 1987) would have been found.

Although we are unable to unravel the interactions among all these factors in this observational study, our statistical results suggest that many elements in habitat structure and environment shape the AH community assemblage relevant to a mid-elevation optimum.

Habitat:environment

Habitat factors explain more variance in the AH species assemblage than environmental factors when arid and montane grasslands were examined separately, but environmental factors are co-equal when the grassland types are combined.

Habitat Both plant community composition (AH species assemblages effectively defined by plant community classification) and structure (positive correlations with patterns of diversity and growth forms) influenced AH community assemblages. Similar findings were reported from Auchenorrhynchan surveys throughout northern England and Scotland (Eyre et al. 2001). The emergence from our sample data of plant species density as a significant factor overall, and in separate sequential analysis of arid and montane grasslands, highlights a key role for plant alpha diversity in shaping AH community structure in the central Tien Shan. The contributions of habitat physiognomic factors in AH community structure such as total percent cover, and cover of woody species (as with Eyre et al. 2001) and, with marginal significance, sedges and C_4 grasses are not surprising given the fundamental

differences in vegetation structure between arid and montane grasslands (Taft et al. 2011).

Our results contrast with findings from a study of Lepidoptera habitat–environment relations in California (Hawkins and Porter 2003) which examined broad patterns from published datasets and found environmental factors to outweigh habitat in explaining Lepidoptera species associations; however, sample data were not closely coordinated. Experimental controls on vegetation structure in a local study of leafhopper community organization found vegetation architecture, rather than plant composition, to be a predominant factor in explaining leafhopper species assemblages (Brown et al. 1992). However, in a local observational study, plant species composition was found to be more influential than emergent properties of the vegetation in explaining patterns of AH species assemblages (Novotny 1990). Although we did not record plant height to augment our habitat structure parameters, species identity may serve as a reasonable proxy because these factors are likely auto-correlated across the geographic scale and ambient land use practices at our study sites.

Environment Elevation and covariate M. A. Temperature were the most prominent environmental factors in explaining plant species assemblages associated with our study sites (Taft et al. 2011). Overall, Elevation (and correlate M. A. Temperature), M. A. Precipitation, and Season are the major environmental factors structuring the AH community assemblages. Partitioning of the two broad habitat groups revealed that Precipitation and Season predominate in arid grasslands whereas Elevation, Longitude, and Season predominate in montane grasslands. Elevation effects are confounded by multiple environmental factors, some altitude dependent such as temperature and atmospheric pressure, and others somewhat independent of altitude such as hours of sunshine, wind, geology, available moisture, and land use (Körner 2007). Exclusive to montane grasslands, Longitude was the geographic variable that contributed to explained variance in the AH species assemblage, contrasting with results for multiple species surveys in the southern Appalachians (McCoy 1990) where Latitude was an important factor. Perhaps these differences can be attributed to the predominately east–west orientation of the Tien Shan (and Kyrgyzstan) compared with the north–south orientation of the Appalachian Mountains.

Patterns of insect communities at local scales have demonstrated contrary or no trends with altitude (Hodkinson 2005); however, at broader regional scales, mid-elevational peaks have been found for many species groups including Auchenorrhyncha (McCoy 1990). Scale of sample extent and grain size can contribute to the variable interpretations of observations (Rahbek 2005). In our study, grain size being equal, as ecological extent of the

analysis is increased by combining arid and montane grasslands, environmental factors gain in proportion of explained variance.

Our results suggest that a combination of habitat and environmental factors contribute to explain variance in AH community assemblages in the central Tien Shan. However, despite the similar environmental influences on both AH and plant communities and concordance in community structure, substantial unexplained variance in AH community composition remains in the model. This outcome is similar to the controlled experiment by Brown et al. (1992).

Ecological dark matter

No studies we are aware of have examined interactions between AH and plant communities from such closely coordinated species-level samples taken across a broad ecoregion such as grasslands of the central Tien Shan Mountains; hence, we are unable to say whether the level of explained variance in the stepwise distance-based linear model is more or less than expected. The unexplained variance, due presumably to individualistic species responses to extrinsic (e.g., past and present land use, season of sample) and intrinsic factors (e.g., competition, predation), *sensu* Gleason (1926), exceeds what is suggested in the model. As evidence, 28% of AH species had occurrences in both arid and montane vegetation classes; however, only 5.6% were dominant within classes in both vegetation types and only 3.6% were indicator species in both groups.

Land uses likely to influence AH species assemblages include grazing (Morris 1971; Brown et al. 1992), haying (Morris 1981; Lawton 1983), woody encroachment (habitat loss), and fire (Warren et al. 1987; Siemann et al. 1997), factors that also greatly influence the community structure of grassland and savanna habitats. Grazing and haying are the major land use in Kyrgyz grasslands, and unlike many grassland areas, woody encroachment and burning appear negligible. Grazing has been shown to be a limiting factor in microarthropod populations and diversity (Dennis et al. 1998). Previous studies have found that grazing effects on insect communities are associated with alterations to habitat structure and species diversity (Morris 1967; Gibson et al. 1992; Brown et al. 1992). All sites in the current study were open range and grazing was ongoing or apparent at several study sites. However, since details of the grazing history are unknown (e.g., frequency, intensity, duration), we are unable to estimate the influence of grazing on interactions between vegetation and AH communities. AQI has been found to be a reliable indicator of AH community integrity (Wallner et al. 2013a, b) and sensitive to grazing effects (Frei et al. 2014). However, AQI

scores were not a good predictor of sites where grazing was underway at the time of our samples. In this study, AQI scores primarily distinguish montane from arid grassland sites.

Predation and parasitism are major additional factors structuring AH communities (Waloff 1980). In experimentally controlled grassland habitat structure, associate predator and parasite assemblages explained greater variance in total arthropod diversity compared to plant diversity (Siemann et al. 1998). However, Kruess and Tscharrntke (2002) found no change in predator–prey ratios in insect faunas including Auchenorrhyncha in intensively grazed pastures. We did not explicitly measure abundances of predators and parasitoids in our insect transect samples, but nearly all samples appeared to include substantial numbers of Trichogrammatidae and Mymaridae, wasps that parasitize AH eggs as well as more general predators, particularly various true bugs (Nabidae, Reduviidae, Miridae) and spiders.

Conclusions

From closely linked sample data, AH and plant communities in the central Tien Shan appear to be highly correlated in terms of community architecture. However, individualistic species responses to biotic and abiotic gradients limit the degree to which AH species assemblages can be accounted for by the habitat and environmental factors measured in this study. Changes in AH community structure with climate warming can more predictably address patterns of species richness than species composition. If the mid-elevation optimum is narrowed, there likely will be a net loss of AH biodiversity.

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