

## ORIGINAL CONTRIBUTION

**Long-term population trends in three grassland insect groups: a comparative analysis of 1951 and 2009**S. Schuch<sup>1</sup>, J. Bock<sup>1</sup>, B. Krause<sup>2</sup>, K. Wesche<sup>3</sup> & M. Schaefer<sup>1</sup><sup>1</sup> Animal Ecology, Johann-Friedrich-Blumenbach-Institute of Zoology and Anthropology, Georg-August-University of Göttingen, Göttingen, Germany<sup>2</sup> Plant Ecology, Albrecht-von-Haller-Institute for Plant Sciences, Georg-August-University Göttingen, Göttingen, Germany<sup>3</sup> Senckenberg Museum of Natural History Görlitz, Görlitz, Germany**Keywords**

abundance, Auchenorrhyncha, Heteroptera, Orthoptera, species composition, species richness

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**Abstract**

Development of farming practices has caused drastic changes in European agricultural landscapes during the past 50 years. As a consequence of these changes, insect diversity is widely expected to decline. We performed a comparative analysis with long-term data of three insect groups: Auchenorrhyncha, Heteroptera and Orthoptera. In 2009, we revisited nine grassland sites in northern Germany that were originally sampled in 1951 using the same techniques and during a similar time frame. We found that the insect community exhibited no consistent trends between years. Species richness of Auchenorrhyncha and Heteroptera increased on plot level as well as on landscape level but remained unchanged for Orthoptera. Abundance of Auchenorrhyncha and Orthoptera significantly decreased, while Heteroptera increased. There is a strong trend towards homogeneity in community composition for Heteroptera and a weak one for Auchenorrhyncha. The frequency and abundance of species preferring disturbed and/or eutrophic habitats increased, whereas the number of species preferring low-productive habitats declined. This trend is especially pronounced in Auchenorrhyncha. Generalistic species were more abundant in relative proportions as well as in absolute numbers. We hypothesize that these trends arise from alterations of Central European landscapes because of agricultural intensification over the last several decades.

**Introduction**

Agriculture has drastically changed the natural landscape of Europe during the past 60 years, particularly in grassland habitats. In large areas of northern Germany, more than 50% of the original wet meadows that existed in the 1950s and 1960s are gone (Wesche et al. 2009). Of the extant grasslands, more than 80% are intensively used and species-poor (Krause et al. 2011). Such strong declines of oligotrophic grasslands also occurred in other European countries such as the Czech Republic (Prach 2008), England (Treweek et al. 1997) and Hungary (Joyce and Wade 1998). As a consequence of shifts in land use, insect diversity in these habitats is widely

expected to decline (Watkinson and Ormerod 2001; Biedermann et al. 2005). Indeed, there is ample evidence that more intensive agricultural practices, such as mowing, grazing or fertilization, result in changes in species occurrence, community structure and diversity of insects (Morris 1981; Prestidge 1982; Kruess and Tschardtke 2002; Nickel and Hildebrandt 2003). Haddad et al. (2000) found that increased nitrogen deposition indirectly caused auchenorrhynchan species richness to decline via decreased plant species richness. This type of loss could potentially create homogeneous insect communities because of a general decline in habitat diversity or also decrease number of specialists because of the loss of specific host plants.

Support for the idea that altered land-use practices affect insect communities comes from many studies that demonstrate a decline in insect diversity during the last decades (Conrad et al. 2004; Thomas et al. 2004; Biesmeijer et al. 2006), and it has been suggested that land-use intensification may now be having a greater impact on common, generalist species (Van Dyck et al. 2009). While trends in species richness are seemingly obvious, these are not necessarily analogous to trends in insect abundance, which are far less clear. Losses in common species are largely going undetected until they cause local extinction (Gaston and Fuller 2007). The problem is especially severe in invertebrate communities, where few data are available. This lack of long-term records of insect abundance is related to the sparseness of data from the 1950s to the 1970s, when only a few entomologists used standardized sampling methods and conducted reproducible studies. There are only a few assessments of truly long-term changes (considering at least three decades) in insect abundance in Central Europe, and those available usually cover only single taxa. Conrad et al. (2004) studied common macro-moths of Great Britain with data covering 35 years and found that 54% of the species significantly decreased in abundance, while just 22% increased. A study from Bavaria demonstrated that the number of night-active butterflies from standardized light-trap captures continuously decreased from approximately 250 individuals per month in 1969 to 50 in 1995 (Reichholf 2005), while species richness remained largely unaffected. This study suggests that a strong decline in insect populations can remain undetected if just species richness is considered.

To reveal trends in insect abundance and richness, we present a comparative study with original data from a grassland survey conducted in 1951 (Marchand 1953). Marchand used standardized sweep netting, which is easily mimicked and thus comparable for abundance data, and he examined three insect groups: Auchenorrhyncha (planthoppers and leafhoppers), Heteroptera (true bugs) and Orthoptera (grasshoppers and bush crickets). These three groups are very abundant in grasslands and constitute the dominant herbivore groups, with Auchenorrhyncha at densities frequently exceeding 1000 individuals per square metre (Waloff and Thompson 1980; Nickel and Hildebrandt 2003). The ecology of Central European Auchenorrhyncha species is well known, including over-wintering stage, voltinism (number of generations per year) or the range of host plants (Nickel 2003). Similarly, extensive ecological information is available for Heteroptera

(Wachmann et al. 2004). We used information about species characteristics to interpret long-term changes in species abundance; for example, how the ratio of specialists to generalists changed. We also analysed historical and current aerial images and took vegetation samples to quantitatively assess driving factors of faunal change.

Specifically, we asked the following questions: (i) Are there substantial long-term developments in the diversity and abundance of the three investigated grassland insect groups?; (ii) Are there patterns in the species composition of these groups which suggest land-use intensification to be a crucial factor for long-term changes?; (iii) Are changes in local plant communities or landscape-level habitat characteristics able to explain developments in the investigated insect communities?

## Material and Methods

### Study sites and sampling

To perform a comparative analysis of auchenorrhynchan (A), heteropteran (H) and orthopteran (O) communities, we sampled at nine of the original 12 sites that were studied between May and October 1951 (Marchand 1953). All sites are located near Stolzenau and Leese (Lower Saxony) in the lowlands of northern Germany. Marchand selected his sites according to a moisture gradient with the result that there are three types of habitat (table 1): (i) dry grassland (sites I and II), (ii) mesic grassland (sites III–IV) and (iii) moist grassland (sites X–XII). The mode and extent of agricultural land use were also recorded. Four of the plots were not mown or grazed in 2009, while in 1951 each plot was mown at least once a year (table 1). Marchand gave brief descriptions of the plant communities present in 1951, which were helpful in rediscovering the plots. Some of these plots have changed severely during the past 60 years. Three sites (VII, VIII and IX) had been converted to arable fields since 1951 and could not be included in the study. In all other cases, sufficiently similar habitats were still present to permit sampling. The weather in both sampling periods was largely comparable: the mean annual precipitation of Germany was 751 mm in 1951 and 813 mm in 2009 (data received from Deutscher Wetterdienst). Mean spring and summer precipitation slightly differed by 7 and 8 mm between both periods. In contrast, mean autumn precipitation was 48 mm higher in 2009 when compared with 1951. Mean annual temperature rose from 8.7°C in 1951 to 9.2°C in 2009.

**Table 1** Land use and vegetation types (community and alliance) for nine different plots near Stolzenau, sampled in 1951 and sampled again in 2009

Land-use practices			Vegetation			
			Community		Alliance	
1951	2009	1951	2009	1951	2009	
<i>Dry</i>						
I	Sheep grazing	Ungrazed	<i>Corynephorum cladonietosum</i>	<i>Arrhenatheretum elatioris</i>	<i>Corynephorion canescentis</i>	<i>Arrhenatherion elatioris</i>
II	Sheep grazing	Ruderalized	<i>Corynephorum agrostidetosum</i>	<i>Corynephorum agrostidetosum aridae</i>	<i>Corynephorion canescentis</i>	<i>Corynephorion canescentis</i>
<i>Mesic</i>						
III	Mown twice	Paddock	<i>Arrhenatheretum elatioris</i>	<i>Ranunculus repens</i> – <i>Alopecurus pratensis</i> comm.	<i>Arrhenatherion elatioris</i>	<i>Arrhenatherion elatioris</i>
IV	Mown twice	Ruderalized (horses)	<i>Arrhenatheretum elatioris</i>	<i>Ranunculus repens</i> – <i>Alopecurus pratensis</i> comm.	<i>Arrhenatherion elatioris</i>	<i>Arrhenatherion elatioris</i>
V	Mown twice	Mown once (edges)	<i>Arrhenatheretum elatioris</i>	<i>Arrhenatheretum elatioris</i>	<i>Arrhenatherion elatioris</i>	<i>Arrhenatherion elatioris</i>
VI	Mown twice	Cattle grazing	<i>Arrhenatheretum elatioris</i>	<i>Arrhenatheretum elatioris</i>	<i>Arrhenatherion elatioris</i>	<i>Arrhenatherion elatioris</i>
<i>Moist</i>						
X	Mown twice	Mown twice	<i>Bromus racemosus</i> – <i>Senecio aquaticus</i> comm.	<i>Ranunculus repens</i> – <i>Alopecurus pratensis</i> comm.	<i>Calthion palustris</i>	<i>Arrhenatherion elatioris</i>
XI	Mown twice	Mown twice	<i>Bromus racemosus</i> – <i>Senecio aquaticus</i> comm.	<i>Ranunculus repens</i> – <i>Alopecurus pratensis</i> comm.	<i>Calthion palustris</i>	<i>Arrhenatherion elatioris</i>
XII	Mown once	Mown twice	<i>Cariceto canescentis</i> – <i>Agrostidetum caninae</i>	<i>Phragmitetum australis</i>	<i>Caricion nigrae</i>	<i>Phragmition australis</i>

Hereby, mean spring temperature was much lower in 1951 than in 2009 (7.0/9.9°C), whereas mean summer and autumn temperatures only slightly differed (both 0.7°C warmer in 2009 than in 1951).

We sampled eight times at each site beginning in May and ending in September 2009, trying to match sampling dates of Marchand as closely as possible (Appendix S1). Marchand sampled with a sweep net (Ø 30 cm; 100 beats per sampling); we used the same method and assume that comparisons between years are justified. Research has shown that transect surveys by different teams at the same sites but on different routes may produce similar rankings in insect species abundance (Schlicht et al. 2009). For A and H, sampling by sweep net is an adequate technique to obtain reliable information about insect community composition and abundance in grassland and scrub habitats (Törmälä 1982; Buffington and Redak 1998; Standen 2000). For O, the use of sweep nets is less effective and it is recommended to supplement sampling with other methods such as acoustical surveys.

No other methods besides sweep nets were employed in 1951, and therefore, only sweep nets were used in 2009; as a result, information on species identity in O communities should be considered with caution. However, recent work indicates that using sweep nets to sample O can still be valid in comparisons of abundance (Gardiner et al. 2005).

Only some vegetation samples from the 1950s were available. In 2009, in each site we sampled one 10 × 10 m plot and recorded all vascular plants and an estimate of their cover along with exact locality information. We compared aerial photographs of the 1950s with photographs from 2008 to assess the development of the vegetation in the plots and their immediate surroundings, i.e. changes in size of arable fields, wood cover and grassland cover. We compiled relevant life history traits for each species based on the studies by Nickel (2003) and Wachmann et al. (2004). For A, we examined four traits: degree of host plant specialism (monophagous: one host plant species; second degree monophagous: one

host plant genus; oligophagous: one host plant family; second degree oligophagous: two host plant family or up to four host plant species each belonging to up to four different families; polyphagous: various host plants from many different families), voltinism (usually one or two generations per year), over-wintering stage (egg, nymph or adult) and dispersal ability (flightless short-winged brachypterous or mobile long-winged macropterous morphs). For H, we included habitat requirements (preference for dry, mostly dry, dry or wet, mostly wet or wet conditions), over-wintering stage (egg or adult; over-wintering juveniles were not present), feeding type (phytophagous, phytozoophagous or zoophagous) and voltinism. For O, species identity and ecological characteristics were not considered.

**Data analysis**

We calculated estimates of alpha ( $\alpha$ ), beta ( $\beta$ ) and gamma ( $\gamma$ ) species richness first considering only species presence/absence and second using species abundance. When considering presence/absence,  $\alpha$  species richness was defined as plot-level species richness, Whittaker's  $\beta$  species richness (total number of species/mean species richness) was used as a simplified definition of among-plot differentiation (Tuomisto 2010) and  $\gamma$  species richness was used to denote the total number of species caught in each year. Abundance was considered at both the plot level and for the entire sample. Combining species numbers and abundance values,  $\alpha$  Shannon diversity was used to describe plot-level patterns, mean Bray–Curtis distance among samples provided an estimate for among-plot differentiation, and  $\gamma$  Shannon diversity (based on the total sample) was used to describe diversity on the landscape level.

Data were visualized using detrended correspondence analysis (DCA), which provided evidence for moderately long faunistic gradients [length of gradient = 3.1 and 4.1, equivalent to less than one species turnover, (McCune et al. 2002)] and prompted us to use asymmetric dissimilarity measures (Sørensen/Bray–Curtis similarity). We used boxplots (median and interquartile ranges) to summarize data on species abundance per year and insect group. Differences were tested with Wilcoxon test (paired samples). We used an indicator species analysis to test for species that were significantly associated with one sampling period or the other (Dufréne and Legendre 1997). Relationships between A and H communities in 1951 and 2009 were tested with a Mantel test (Bray–Curtis similarity). Data were anal-

ysed using R (R Development Core Team) and PC-ORD (McCune and Mefford 2006).

**Results**

**Community composition**




We detected 94 species with 21 887 individuals of Auchenorrhyncha (A), 88 species with 3246 individuals of Heteroptera (H) and 15 species with 460 individuals of Orthoptera (O) in 1951 and 2009 combined.

When considering presence/absence, only H showed a significant increase in  $\alpha$  species richness ( $V = 5$ ,  $P = 0.04$ , table 2).  $\beta$  species richness slightly increased for A [1951: 2.8; 2009: 3 and O (3 and 3.7)] for A and O but decreased for H (3.7–3.1). Total species numbers increased for all three groups; in 2009, they were 36% higher in A and 20% each in both H and O.

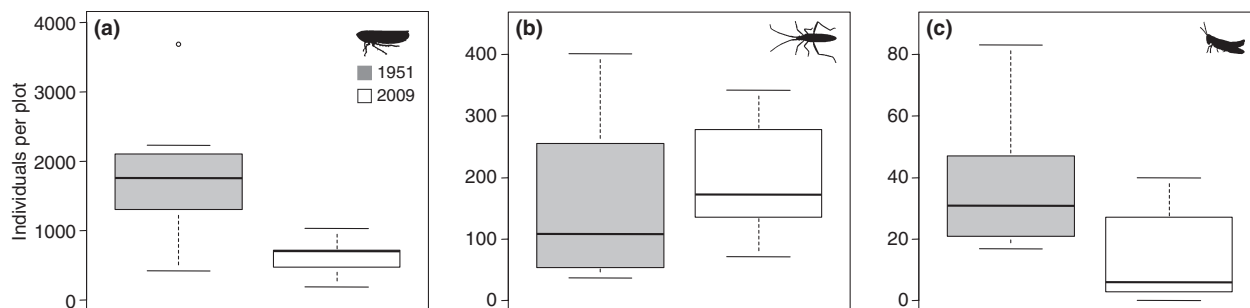
Median numbers of individuals per plot declined significantly in both A and O (fig. 1a,c; table 2, A:  $V = 44$ ,  $P = 0.01$ ; O:  $V = 43$ ,  $P = 0.01$ ), while median numbers in H significantly increased (fig. 1b; table 2,  $V = 45$ ;  $P = 0.004$ ). Total numbers of individuals of A and O exhibited strong declines by about 64% each, while H increased by about 28%.

Plot-level-based Shannon diversity did not change significantly over time for any of the three groups. Mean Bray–Curtis distances [abundances were  $\log(x + 1)$  transformed] declined from 0.61 to 0.57 in A, from 0.75 to 0.55 in H and increased from 0.77 to 0.83 in O. Ordinations for A (fig. 2a) as well as for H (fig. 2b) indicated that the species composition in 2009 was less heterogeneous than in 1951. In the

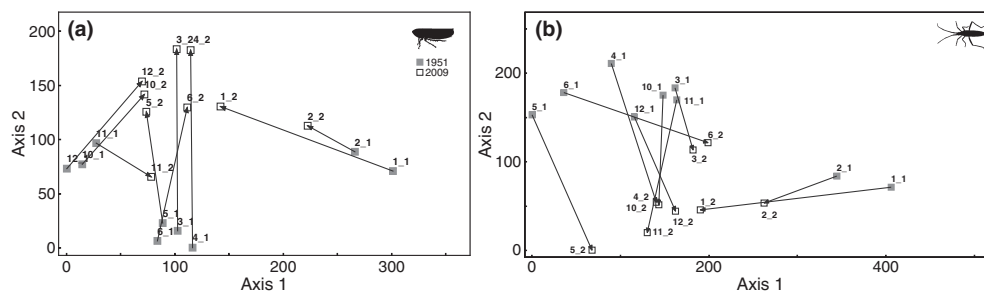
**Table 2** Total number and medians of species (s) per plot; beta species richness, total number and medians of individuals (i) per plot (first to third line: Auchenorrhyncha, Heteroptera and Orthoptera). Numbers refer to sweep net samples from 1951 and 2009 (eight samples each year, 100 sweeps per visit)

	Total #s		Median #s		$\beta$ species richness		Total #i		Median #i	
	1951	2009	1951	2009	1951	2009	1951	2009	1951	2009
		55	75	20	25	2.8	3.0	16 088	5799	1762
	52	63	14	19	3.7	3.3	1426	1820	108	172
	9	11	3	3	3.0	3.7	335	125	31	5

#s, Number of species; #i, number of individuals.



**Fig. 1** Boxplots showing mean number of individuals on plot-level for the whole sampling periods of 1951 and 2009; Auchenorrhyncha (a), Heteroptera (b) and Orthoptera (c).



**Fig. 2** Detrended correspondence analysis ordinations of insect communities at the nine different plots [all species, abundance  $\log(x - 1)$  transformed, downweighting of rare species, detrending by segments]. (a) Auchenorrhyncha (eigenvalue/length of gradient axis 1: 0.49/3.1; axis 2: 0.24/1.8; axis 3: 0.09/1.9). (b) Heteroptera (eigenvalue/length of gradient axis 1: 0.57/4.1; axis 2: 0.21/2.1; axis 3: 0.12/1.8).

DCAs, the plot records of 2009 clustered more and the records of 1951 are more widely distributed in the ordination space. For example, in 1951 differences between plot I (dry habitat) and plot X (wet habitat) for both A and H corresponded to about one species turnover along the main axis (about four SD-units), while dissimilarities between the same plots in 2009 were half that large (less than two SD-units). The pattern was similar for presence/absence data (graphs not shown). For O, there was also a weak trend for homogenization.  $\gamma$  Shannon diversity for the entire data set declined clearly in A, while it remained somewhat constant in H and O.

Mantel tests comparing the relationship between pair-wise auchenorrhynchan Sørensen dissimilarity and heteropteran Sørensen dissimilarity indicated a strong correlation in 1951 ( $r_M = 0.71$ ,  $P = 0.003$ , 4999 permutations), while the relationship in 2009 was not as strong ( $r_M = 0.42$ ,  $P = 0.036$ ).

### Individual species

Frequency and abundance of several species differed significantly between the 2 years (table 3). Two A species, *Balclutha punctata* and *Zyginidia scutellaris*, did not occur in 1951, but were present on every plot in



2009. *Dicranotropis hamata* and *Psammotettix alienus* did not occur in 1951, but were found in 56% of all plots in 2009; *Macrosteles sexnotatus* and *Psammotettix confinis* were also significantly more common in 2009. *Xanthodelphax straminea* was not present in 1951, but occurred in 44% of 2009 samples. In contrast, two formerly common species (frequency >65%), *Elymana sulphurella* and *Forcipata forcipata*, completely disappeared, and *Athysanus argentarius* declined from 67% to 22%. The usually very common species *Jassargus pseudocellaris*, *Philaenus spumarius* and *A. argentarius* decreased in abundance and frequency.

Among H, only 7 of 88 species underwent changes; all of them increased in numbers from 1951 to 2009. *Amblytylus nasutus*, *Aelia acuminata* and *Dolycoris baccarum* did not occur in 1951, but were present in more than two-thirds of all samples of 2009. The frequencies of *Leptopterna dolabrata*, *Megaloceroea recticornis* and *Capsus ater* also increased markedly.

### Species characteristics

In 2009, about 12% of A individuals were monophagous (summed first and second degree), whereas their proportion had been 30% in 1951 (table 4). Relative



**Table 3** Frequency (%) and number of individuals of auchenorrhynchan and heteropteran species with marked differences between 1951 and 2009

	Frequency (% of all plots)		Individuals (per nine plots)		P
	1951	2009	1951	2009	
					
<i>Balclutha punctata</i>	0	100	0	47	0.001*
<i>Zyginidia scutellaris</i>	0	100	0	332	0.001*
<i>Elymana sulphurella</i>	67	0	288	0	0.008*
<i>Eupteryx notata</i>	67	0	17	0	0.009*
<i>Forcipata forcipata</i>	67	0	185	0	0.009*
<i>Jassargus pseudocellaris</i>	100	67	1154	209	0.018*
<i>Macrosteles sexnotatus</i>	67	89	8	410	0.019*
<i>Athysanus argentarius</i>	67	22	100	4	0.021*
<i>Dicranotropis hamata</i>	0	56	0	39	0.023*
<i>Psammotettix alienus</i>	0	56	0	42	0.033*
<i>Philaenus spumarius</i>	78	44	886	18	0.033*
<i>Psammotettix confinis</i>	78	100	61	323	0.050*
<i>Megadelphax sordidula</i>	78	56	1368	47	0.065(*)
<i>Cercopis vulnerata</i>	0	44	0	15	0.068(*)
<i>Javesella pellucida</i>	100	100	2031	823	0.073(*)
<i>Javesella dubia</i>	0	44	0	23	0.082(*)
<i>Xanthodelphax straminea</i>	0	44	0	34	0.083(*)
<i>Florodelphax leptosoma</i>	44	0	409	0	0.086(*)
<i>Megamelus notula</i>	44	0	126	0	0.088(*)
<i>Stenocranus major</i>	0	44	0	7	0.08(*)
					
<i>Amblytylus nasutus</i>	0	78	0	261	0.004*
<i>Stenodema calcarata</i>	78	100	24	144	0.004*
<i>Stenodema laevigata</i>	44	100	15	119	0.005*
<i>Leptopterna dolobrata</i>	11	78	2	76	0.006*
<i>Capsus ater</i>	11	67	2	39	0.011*
<i>Megaloceroea recticornis</i>	11	78	2	71	0.011*
<i>Aelia acuminata</i>	0	67	0	33	0.011*
<i>Dolycoris baccarum</i>	0	56	0	5	0.036*
<i>Stenotus binotatus</i>	11	56	4	108	0.053(*)
<i>Nabis pseudoferus</i>	89	100	22	72	0.074(*)

Indicator species analysis, \* indicating significant differences between years at  $P < 0.05$ , and (\*) trends at  $0.1 > P > 0.05$ .

number of oligophagous and polyphagous individuals increased, while absolute numbers decreased for all A feeding groups. The relative proportion of macropterous individuals slightly increased as well as relative proportion of bivoltine species. Adult over-wintering A occurred in 2009, but were completely absent in 1951. For H, number of individuals with dry habitat requirements decreased over time in relative as well as absolute numbers (table 4). Absolute numbers increased for nearly all ecological groups of H (except for bivoltine species); however, the relative numbers of bivoltine individuals and those over-wintering as

**Table 4** Ecological characteristics of Auchenorrhyncha and Heteroptera from 1951 and 2009, calculated for the sum of all individuals. First, Auchenorrhyncha: degree of host plant specialism (for explanations see text), voltinism (generations per year), overwintering stage and dispersal ability (short-winged = brachypterous; long-winged = macropterous). Second, Heteroptera: habitat requirements, voltinism, feeding type, overwintering stage

Ecological characteristics	Individuals		In %	
	1951	2009	1951	2009
				
Total	16 088	5799		
Host range				
Monophagous	2794	511	17	9
M. 2nd degree	1981	183	12	3
Oligophagous	7638	3464	47	60
Olig. 2nd degree	438	150	3	3
Polyphagous	3237	1491	20	26
Dispersal ability				
Brachypterous	4764	1370	30	24
Macropterous	11 324	4429	70	76
Generations per year				
One	3784	680	24	12
1.5	2806	863	17	15
Two	9498	4256	59	73
Over-wintering stage				
Egg	11 221	4066	70	70
Nymph	4867	1326	30	23
Adult	0	407	0	7
				
Total	1426	1820		
Habitat requirements				
Dry	491	287	34	16
Mainly dry	53	145	4	8
Dry and wet	760	1090	53	60
Mainly wet	82	256	6	14
Wet	40	42	3	2
Feeding type				
Phytophagous	1293	1621	91	89
Zoophytophagous	27	46	2	3
Zoophagous	106	153	7	8
Generations per year				
One	753	1155	53	63
Two	673	665	47	37
Over-wintering stage				
Egg	561	953	39	52
Adult	865	867	61	48

In %, percentage of the total numbers of individuals.

adults decreased. The relative proportion of the trophic types did not differ between years.

**Insect habitat specificity**

In 2009, detailed vegetation samples were available that allowed us to test the extent of habitat specificity

of A and H. The Mantel test of Sørensen dissimilarities in current plant community composition and A communities yielded an  $r_M$  of 0.75 ( $P < 0.001$ ), while for H the  $r_M$  was 0.21 ( $P > 0.1$ ). This indicates that H communities in 2009 were less specific with respect to vegetation communities.

### Vegetation and surrounding landscape

In 1951, two sites were dry sandy grasslands with *Corynephorus canescens*; only one of these was preserved while the other one became ruderalized with an increase in mesic plant species (table 1). The mesic *Arrhenatherum elatius* grasslands remained relatively unchanged and still belong to the same phytosociological alliance. The two wet meadows with *Bromus racemosus* developed into a mesic *Arrhenatherum elatius* grassland, and the moistest stand, which formerly was dominated by small sedges, such as *Carex canescens*, has fallen fallow and is now dominated by *Phragmites australis*.

On the basis of these data, we calculated a rank-based index of phytosociological similarity (same community, different community, different alliance, etc.). In A, changes in Sørensen dissimilarity on a given plot over time (abundance log-transformed) were rank-correlated with changes in phytosociological classifications ( $\rho = 0.67$ ,  $P = 0.05$ ), while changes in H were not related to changes in the vegetation ( $\rho < 0.01$ , ns).

Analysis of aerial photographs indicated that few major structural changes occurred in the last 60 years concerning cover of woody perennials or agriculturally used land.

### Discussion

We aimed to detect long-term changes in species richness, species composition and abundance of insect communities in grasslands that were mainly used as pastures. Two conspicuous trends are apparent: species richness was mostly unchanged whereas overall population density tended to decline. In addition, insect communities became more homogenous and the percentage of generalists increased.




### Community composition

In contrast to previous studies (Conrad et al. 2004; Thomas et al. 2004; Biesmeijer et al. 2006), we did not observe a general decline in insect diversity during the past several decades.  $\alpha$  and  $\gamma$  species richness of A and H increased from 1951 to 2009, while orthopteran

species richness remained almost constant (table 5). We have recently documented a similarly constant O diversity for dry grasslands in eastern Germany over a similar time period (Schuch et al. 2011), indicating that O are relatively tolerant to environmental changes. However, temporal trends of species richness in the more specialized Rhynchota are not that easily explained. Both A and H appear to have benefited from landscape change, but DCA and  $\beta$  species richness, especially for H, suggest that communities have become more similar. Such homogenization trends are in line with general observations for European flora (Smart et al. 2006) and parts of insect fauna (Ekroos et al. 2010). Most notably, these trends were also observed for the flora of the Central European grasslands of the studied region (Wesche et al. 2009).

$\beta$  Diversity (mean Bray–Curtis distance) and  $\gamma$  Shannon diversity clearly decreased during the last 60 years. This decline is because of the second major trend in A communities, where abundance was significantly lower even for formerly dominant, common and widespread species. In 2009,  $\alpha$  Shannon diversity and mean Bray–Curtis distance of O were higher, while their abundance was significantly lower. The loss in abundance of A and O may indicate a long-term decline, although with only 2 years in our study it is difficult to make definite conclusions. Studies indicate that planthopper populations fluctuate strongly within and among seasons in the same patch as well as among spatially distant patches (Denno and Roderick 1990). Müller (1978) found that A diversity can be surprisingly constant, with strong fluctuations in the abundance of single species. Hollier et al. (2005) demonstrated that the local

**Table 5** Comparison of species richness, Shannon diversity (and mean Bray–Curtis distance) and population density of Auchenorrhyncha, Heteroptera and Orthoptera for the years 1951 and 2009

	Species richness			Shanon diversity			Abundance	
	$\alpha$	$\beta^*$	$\gamma$	$\alpha$	$\beta^{**}$	$\gamma$	PL	LL
	(+)	(+)	+	(+)	(-)	-	-	-
	+	-	+	(+)	-	(+)	+	+
	=	=	(+)	+	+	=	-	-

\*Whittaker's  $\beta$ ; \*\*mean Bray–Curtis distance; PL, plot level, LL, landscape level; +, increase; -, decrease; =, no change; brackets indicate weak or non-significant (if tested) trends.

plant community and geographical location had a high explanatory value for the composition of communities of A, while the influence of period was small, even though single species abundance differed between years. We recently compared A communities from eastern German dry grasslands between 1964–1966 and 2008–2010. Numbers of individuals were lower in the second period for any year to year comparison (unpublished data), adding to the evidence for an overall decline of auchenorrhynchan densities. The Mantel tests, and univariate analyses imply that the different insect groups behaved at least partly different, rendering it unlikely that the decline of A and O is caused only by unfavourable climatic conditions in 2009.

The communities of A and H were more closely correlated in 1951 than they are today. The sparse vegetation data yielded sufficient information about changes in the plant communities. Even though our approach is crude, we still detected a significant response of A, while H composition was not correlated with vegetation change. In general, A communities are more closely linked to the vegetation, because many species depend on special host plants. H communities are now more strongly dominated by species that are less dependent on special vegetation.

In H, the most common species in 2009 were as frequent as in 1951, and several generalist species became more dominant. In accordance with our data, Di Giulio et al. (2001) found that intensively managed meadows were dominated by more widespread and less specialized H species.

### Species and their ecological characteristics

A and H species that prefer disturbed and eutrophic sites increased, whereas species occurring on low-productive sites decreased. This trend is evident in terms of both frequency and number of individuals and appears to be rather independent from annual fluctuations in abundance. For A, the omnipresence of *Z. scutellaris* and *B. punctata* in 2009 is notable because these species did not occur in 1951. Both species inhabit many types of habitats, with *Z. scutellaris* preferring dry ruderal sites and *B. punctata* moderately shady sites (Nickel 2003). The significant increase in *M. sexnotatus* in 2009 also indicates more ruderalized conditions at present. Marchand caught very few individuals of *Macrosteles* (1‰), while in 2009 about 12% of all individuals belonged to this genus. Species of *Macrosteles* are known to depend on disturbed habitats (Kirby 1992) and to be pio-

neers in fertilized pastures (Nickel 2003). Several other species that prefer disturbed habitats also showed increased densities, including *Dicranotropis hamata*, *Psammotettix alienus* and *Psammotettix confinis*.

In contrast, all A species that significantly decreased (e.g. *Elymana sulphurella*, *Forcipata forcipata*, *Jassargus pseudocellaris*, *A. argentarius* and *Philaenus spumarius*) prefer low-productive habitats (Nickel 2003). These types of habitats are currently disappearing at least partly because of agricultural fertilization. Haddad et al. (2000) found long-term effects of increased nitrogen loading in food plants leading to lowered herbivore insect diversity, but increased abundance. This is in partial contrast to our findings of decreased density of A and O, suggesting that other ecological factors have come into play. One explanation posits that egg mortality may be one of the key factors for the population dynamics of A (Waloff and Thompson 1980). Lower moisture conditions are another known key factor (Kontkanen 1950). The absolute and relative decrease in A monophagous individuals supports the appearance of development towards a more generalized insect community with more oligophagous and particularly polyphagous species. In this context, Novotný (1994) found that average host plant range was wider in ruderal, highly dynamic habitats as compared to more constant habitats. The slight increase in macropterous morphs in 2009 is evidence for the A community being more adapted to dynamic habitats. The increase in bivoltine individuals implies that production of a second generation is advantageous at present times, which might be made possible by a prolonged growing season that lengthened by 5 days from 1951 to 1990 (Menzel et al. 2001; Bale et al. 2002). In climate experiments, Masters et al. (1998) detected an effect of mild winters on the age structure of A, suggesting that these insects mature earlier. They hypothesize that a prolonged activity period could favour bivoltine or multivoltine species. However, in our study, bivoltine species declined in absolute (not in relative) numbers. More data are needed to understand climate change effects on real-world A communities.

For H, the trend towards an increase in species that prefer disturbed and eutrophic sites is not as evident, but there are some parallels. There is a significant increase in individuals of the species *Leptopterna dolabrata* and *Megaloceroea recticornis*, which prefer eutrophic habitats (Wachmann et al. 2004). When all species that increase in abundance are pooled, they account for about 42% of all individuals recorded in 2009. These eight species are



generalists that feed mainly on grasses. In 1951, the same species constituted only 3% of all individuals. Zurbrügg and Frank (2006) also recorded more generalistic H species on meadows and pastures in comparison with more natural areas. Most of these species belonged to the Miridae, which are also the dominant group in our study area. Repeated vegetation surveys from the same region have shown that pastures lost flowering herbs and became more dominated by perennial grasses since the 1950s (Wesche et al. 2009). Species characteristic analysis revealed that the number of H requiring dry habitats decreased, although total number of individuals increased. This suggests that dry habitats were less suitable for H in 2009. It is possible that these habitats became more saturated in recent times, but current data are lacking.

### Conclusion

This study documented several patterns of concern for evaluating the long-term impact of global change on insect communities. First, the assumption of a general long-term decline in insect species richness is not always supported as our study indicates. Global warming can increase survival rates of species migrating to temperate regions (Bale et al. 2002; Hickling et al. 2006), and nitrogen deposition may have positive effects on the individual performance of phytophagous insects (Throop and Lerdau 2004). Both factors can potentially lead to increased species richness. Second, insect abundance is an important measure to assess long-term changes in insect communities. Species richness alone is not sufficient to infer temporal changes. In our study, changes in abundance indicate homogenization and an increased proportion of generalists in insect communities. This may be an indirect effect of land-use change, i.e. because of decreasing plant species richness. Third, relatively similar insect groups respond differently to the same environmental changes as different developments in Auchenorrhyncha and Heteroptera communities suggest. This is important for future work, because the assessment of single insect groups may not allow predicting the development of whole insect communities.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** The complete data is listed for all individuals of Auchenorrhyncha, Heteroptera and Orthoptera sampled on nine sites (for the years 1951 and 2009). Species identity and numbers are given for each site (eight samplings per site and year; 100 sweeps per sampling). Ecological characteristics for Auchenorrhyncha and Heteroptera were also added (explanations for the single traits are fitted in the table).

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