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Community associations of chalk grassland leafhoppers (Hemiptera: Auchenorrhyncha): conclusions for habitat conservation

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Abstract

Due to their confinement to specific hostplants or restricted habitat types, Auchenorrhyncha have the potential to make suitable biological indicators to measure the quality of chalk grassland under different management practices for nature conservation. The Auchenorrhyncha data from a study designed to identify the factors influencing the invertebrate diversity of chalk grasslands in southern England was used to evaluate the potential use of this group of insects as biological indicators. Between 1998 and 2002 altogether 81 chalk grassland sites were sampled. Vegetation structure and composition were recorded, and Auchenorrhyncha were sampled at each site on three occasions in each of two seasons using a 'Vortis' suction sampler. Auchenorrhyncha assemblages were then linked to the different grassland plant communities occurring on chalk soils according to the British National Vegetation Classification (NVC). Altogether 96 Auchenorrhyncha species were recorded during the study. Using data on the frequency and dominance of species, as is commonly done for plant communities, it was possible to identify the preferential and differential species of distinct Auchenorrhyncha assemblages. Significant differences between the Auchenorrhyncha assemblages associated with the various chalk grassland plant communities of the NVC were observed down to a level of sub-communities. We conclude that data on Auchenorrhyncha assemblages can provide valuable information for the setting of conservation management priorities, where data on floristic composition alone may not be sufficient, providing additional information on aspects of vegetation structure and condition.

Introduction

Most grasslands in Britain are plagioclimaxes, needing management to prevent succession into scrub or woodland (Duffey et al. 1974; Rodwell 1992). Chalk grassland in particular is the product of many centuries of extensive grazing, primarily by sheep in the UK. The dryness and infertility of the soil, combined with the effects of grazing, generally result in a plant community of exceptionally high diversity (Rodwell 1992). Chalk grasslands are characterised by a high number of long-lived perennial plants (Grubb 1990) and consequently exhibit high habitat stability over long periods (Odum 1969; Andow 1991). The loss of chalk grassland, considered the most diverse plant community in England, has been particularly great (Keymer and Leach 1990). Over 80% of the lowland calcareous grassland present in the UK in 1949 had been lost or suffered serious damage by the mid 1980s (Newbold 1989). The main causes include the conversion of land for the cultivation of arable crops and the improvement of areas of permanent pasture by the application of fertilisers and pesticides (Blackwood and Tubbs 1970; Keymer and Leach 1990). One of the primary mechanisms for the conservation of remaining areas of chalk grassland in southern England are the Agri-Environment Schemes, supported through EU Regulation 2078/92 (Mortimer et al. 1998). These schemes offer voluntary incentive payments to farmers and other land managers for the adoption of environmentally beneficial farming practices. This study uses data from a comparative study of 81 chalk grassland sites, most of which were being managed under the two main Agri-Environment Schemes, the Environmentally Sensitive Area (ESA) Scheme and the Countryside Stewardship (CS) Scheme. Conservation management on these sites included a limitation in grazing intensity and fertiliser input. The aims of the study were to identify the factors, which most effectively conserve and enhance the biological diversity of existing chalk grasslands or create new areas of such species-rich grassland on ex-arable land, allowing the modification and development of management guidelines for chalk grassland within these schemes. Furthermore, the large scale of the project provided data allowing analysis of the relationship between Auchenorrhyncha assemblages and particular chalk grassland plant communities as defined in the National Vegetation Classification (NVC) (Rodwell 1992). The NVC, although not without flaws, is the most widely accepted and established system to classify plant communities within the UK for the purpose of conservation work and will provide a structural framework for the evaluation of conservation priorities in the foreseeable future. Consequently, research aimed at widening the knowledge about the faunal assemblages associated with NVC communities is essential. Little has been done in this direction although it has already been suggested that the classification methods of the NVC could be used to develop an analogous classification of British ground beetle communities, given sufficient sampling effort within each community (Blake et al. 2003). Here we provide information about the basic parameters of Auchenorrhyncha assemblages within different grassland types linked to the NVC, and the associations of individual species. This was achieved by applying the classical phytosociological approach using data on species frequency and abundance (Braun-Blanquet 1928; Rodwell 1992) to leafhopper assemblages. The resulting description of Auchenorrhyncha assemblages associated with different plant communities provides an excellent source of information regarding the occurrence of biological indicators and target species for decision-makers working in habitat and species conservation.

Biological indicators are taxa or species assemblages which are particularly well matched to specific features of the landscape and demonstrate a predictable response to environmental change (McGeoch 1998; Paoletti 1999; Büchs 2003). For about 25 years the concept of biological indicators has played a major role within nature conservation and the monitoring of environmental conditions (Bick 1982; Kneitz 1980, 1983). However, the use of particular faunal taxa as biological indicators for nature conservation can only be justified if they provide information not described by characteristics of the vegetation, which is relatively easier to monitor. Invertebrates make good biological indicators as a result of their short lifecycles and their often precise and restricted habitat requirements (McLean 1990). Indeed, invertebrates may be better indicators of the ‘health’ of a community than the plant species (Mortimer et al. 1998). Changes in grazing pressure which result in alterations in canopy structure may affect insect assemblages long before changes in plant community composition are manifested (Brown et al. 1990; McLean 1990). This is likely to be especially the case for plant communities such as chalk grassland which are composed largely of long-lived perennials.

Another factor making insects good environmental indicators in grassland systems is that they can show particularly high variation in the species composition of assemblages, as has already been shown for carabids (Luff 1996). Until recently, grassland Auchenorrhyncha were regarded as inferior biological indicators in comparison with some other insect groups, mainly as a result of the paucity of knowledge about their ecology (Spang 1992). However, it has been demonstrated that

Auchenorrhyncha are good organisms to monitor conditions of grassland habitats particularly regarding management history, disturbance or other environmental factors like soil conditions or moisture (Marchand 1953; Emmrich 1966; Andrzejewska 1979; Bornholdt and Remane 1993; Hildebrandt 1995; Nickel and Achtziger 1999; Nickel et al. 2002; Nickel and Hildebrandt 2003). Indeed, by separating leafhopper species into different guilds according to their habitat requirements Auchenorrhyncha indicate different grassland qualities on a rather fine-tuned level (Bornholdt 2002; Maczey 2005).

Methods

Sampling sites

The chalk grassland sites used in the study were drawn from sites selected for long-term monitoring programmes for the ESA and CS Schemes (ADAS 1996, 1997; Carey et al. 2003). Two areas on the chalk soils of southern England are designated as ESAs, the South Downs and South Wessex Downs. These represent areas with high landscape value, in part defined by a high concentration of chalk grassland. In other areas with chalk soils, such as the North Downs and Chilterns, the CS Scheme provides payments to encourage the conservation of remnant patches of chalk grassland (Figure 1). A total of 81 grassland sites were surveyed twice during the course of the project.

The NVC defines seven calcicolous grassland communities (including 25 sub-communities) in southern England (Rodwell 1992). Five of these communities (including 11 sub-communities) were sampled during this study. In addition, four mesotrophic grassland communities occur on chalk soils in southern England in situations where topography or management history have resulted in deeper, moister, more fertile soils. The set of sites included representatives of all four of these communities, covering seven of the 14 sub-communities. An overview of the sampled grassland communities is given in Table 1.

Sampling technique and sample processing

At each site, the invertebrates and the vegetation were sampled three times in a year, in late spring/early summer, mid-summer and late summer/early autumn. ESA sites were sampled in 1998 and 2000; CS sites were sampled in 1999 and 2002. A transect across the site was taken and five equidistant

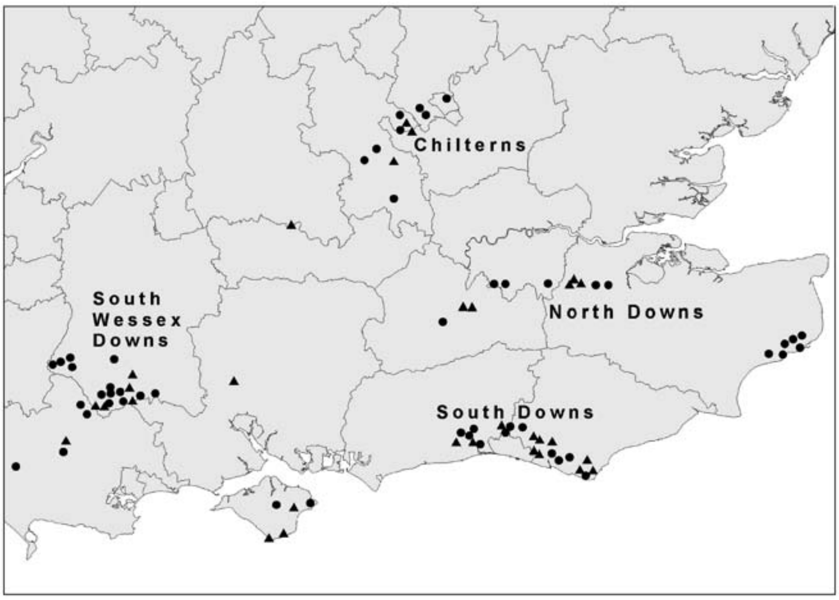

Figure 1. Geographic location of the sites (● calcicolous grasslands, ▲ mesotrophic grasslands).

Table 1. Overview of the sampled grassland communities.

Grassland community	NVC code	Number of sites
Calcicolous grassland	CG	52
Festuca ovina-Avenula pratensis grassland	CG2	37
Cirsium acaule-Asperula cynanchica sub-community	CG2a	14
Succisa pratensis-Leucanthemum vulgare sub-community	CG2b	7
Holcus lanatus-Trifolium repens sub-community	CG2c	16
Bromus erectus (now Bromopsis erecta) grassland	CG3	10
Typical sub-community	CG3a	3
Centaurea nigra sub-community	CG3b	4
Knautia arvensis sub-community	CG3c	1
Festuca rubra-Festuca arundinacea sub-community	CG3d	2
Brachypodium pinnatum Grassland	CG4	2
Holcus lanatus sub-community	CG4c	2
Bromus erectus (now Bromopsis erecta)-Brachypodium pinnatum Grassland	CG5	3
Typical sub-community	CG5a	3
Mesotrophic grassland	MG	29
Arrhenatherum elatius grassland	MG1	5
Festuca rubra sub-community	MG1a	3
Pastinaca sativa sub-community	MG1d	1
number of sites where classification to sub-community level was not possible		1
Cynosurus cristatus grassland	MG5	6
Galium verum sub-community	MG5b	5
Number of sites where classification to sub-community level was not possible		1
Lolium perenne-Cynosurus cristatus grassland	MG6	11
Typical sub-community	MG6a	5
Trisetum flavescens sub-community	MG6c	6
Lolium perenne leys and related grasslands	MG7	7
Lolium perenne-Trifolium repens leys	MG7a	6
Lolium perenne-Poa trivialis leys	MG7b	1

sampling points located along its length. Invertebrates were sampled from these five sampling points. The Auchenorrhyncha were sampled with a 'Vortis'-suction sampler (Burkhard Manufacturing, Rickmansworth, UK). At each sampling point, a sample was obtained by placing the sampler in 15 sampling positions within a radius of 3 m of the centre point and held for 10 s. The total area of turf covered by each sample was approximately 0.3 m^2. During each invertebrate sample, 10 measurements of the vegetation height were taken randomly with a standardised 'drop-disc' (30 cm diameter, 200 g weight, see Stewart et al. 2001). The species composition of the plant community was surveyed within 2×2 m quadrats over the centre of each sampling plot using the Dominance scale.

Table 2. Frequency classes.

Frequency class I	= >0–10%
Frequency class II	= >10–30%
Frequency class III	= >30–5%
Frequency class IV	= >50–7%
Frequency class V	> 70%

Analysis

Auchenorrhyncha assemblages were characterised using the approach usually adopted for plant communities (e.g., Rodwell 1992). To compare assemblages associated with two plant communities (or sub-communities), the order of species using frequency and dominance classes follows simple rules, allowing a quick overview over the key characteristics of the compared communities. Frequency and dominance classes were used as shown in Tables 2 and 3. The species were arranged in blocks according to their pattern of occurrence among the compared grassland types. Within these blocks, species were sorted by decreasing frequency. The first group is made up of the constants, those species occurring in the frequency class IV or V. This is followed by a second block showing the preferential species which are more frequent and usually more abundant in the first grassland type

Table 3. Dominance scale (logarithmic after Engelmann 1978).

6 = eudominant	= 32.0–100%
5 = dominant	= 10.0 < 32.0%
4 = subdominant	= 3.2 < 10.0%
3 = recedent	= 1.0 < 3.2%
2 = subrecedent	= 0.32 < 1.0%
1 = sporadic	= < 1.0%
0 = missing	

compared with the second one. Species with the same frequency class but significant differences of abundance are included here, as well. The next block shows species more frequent or abundant in the second grassland type. The last group of species lists the general associates of similar frequency and abundance in both or of low occurrence in only one of the types.

Preferential species are those, which are typically more frequent and abundant in one grassland type in comparison with another. Species restricted to only one of the compared types can be classified as differential species (Meyer-Cords and Boye 1999). In this study the classification of preferential and differential species follows some simple rules given in Table 4. It should be remembered that the findings presented refer to particular plant communities in southern Britain, and that assemblages may vary when data from other regions and habitats are included.

Wherever it was possible species were provisionally classified as typical chalk grassland, dry grassland, eurytopic or nitrophilic species valid for the southern half of Britain. To avoid autocorrelation this was done purely on the basis of the literature knowledge of their autecology (e.g., Schiemenz 1969; Waloff and Soloman 1973; Cook 1996; Nickel and Achtziger 1999; Nickel 2003) and not through results of this study. Species regularly occupy more than one category. For example, most – although not all – species regarded as characteristic for chalk grassland are equally typical dry grassland species. On the other hand nitrophilic species are seen to prefer grasslands rich in nutrients but may also still regularly occur in other habitats. Since the classification of these species is not based on a detailed analysis due to a lack of data from the British Isles, future studies may lead to a shift of single species into different categories in some cases.

Nomenclature is according to Holzinger et al. (1997) with adaptations from Remane and Guglielmino (2002), Szwedo (2002) and Holzinger et al. (2003).

Table 4. Definition of species classification.

Category	Criteria (adopted and extended after Rodwell et al. 1998)
Constant species	• Species with a frequency value of IV and V in all assemblages are regarded as constant unless there are significant differences in the dominance structure
Preferential species	• Frequency value at least one class higher than in the other compared assemblages • Frequency value at least III • If frequency value is only II or I, the average dominance value has to be at least 2 and the max dominance value at least 3 or there are significant differences in the dominance structure • If the frequency value is the same in compared groups, preferential species can still be described, if the dominance structure is significantly different
Differential species	• Frequency value at least II, average dominance value at least 2 or the max dominance value at least 5 • Species has to be absent in the compared assemblage • If frequency is only I or dominance value species only 1, a species can still be regarded as a differential species if habitat requirements (e.g. host plant appearance) make it most unlikely for the species to be found in the compared assemblage
General associates	• All other species are regarded as general associates of the community or, if not grassland species, as vagrant (xenotopic) species • Species with a higher frequency class in one assemblage but a higher abundance in the other one are regarded as general associates as well

Statistics

The testing of significant differences between species and species groups of the compared plant communities was done using the 'Mann–Whitney *U*-test' using the statistical package SPSS, after converting the raw data into ranks by using the dominance values of each species. This nonparametric test was chosen because of its robustness when dealing with unbalanced data. Correlations were also tested with regression analysis using Excel. Tables displaying columns with the same letter indicate that there are no significant differences between these columns. Due to the low number of available samples from ranker, unmanaged or only extensively managed chalk grassland sites the three NVC communities CG3 (Bromus erectus grassland), CG4 (Brachypodium pinnatum grassland) and CG5 (Bromus erectus-Brachypodium pinnatum grassland) have been combined to avoid working with very unbalanced data and allowing a statistical comparison with the usually grazed and more intensively managed CG2 grassland. The three combined communities show similar plant species composition and structural appearance; their basic differences relate to the abundance of the grasses *Brachypodium pinnatum* and *Bromopsis erecta*. This grassland group will be referred to as CG3–5 grassland.

Results

General results

Of the 96 species occurring on the 81 grassland sites, 84 are typical grassland species. The other 12 taxa belong to polyphagous or oligophagous species feeding on woody shrubs and trees. Of the 84 grassland species, 62 feed almost exclusively on monocotyledonous plants (grasses, sedges and rushes). Only 22 species feed on dicotyledonous forbs (Nickel and Remane 2002). Classified by host specification according to Nickel and Remane (2002) and Nickel (2003) the 84 grassland species can be separated into 11 polyphagous (feeding on more than two plant families), 43 oligophagous (feeding on only one or two plant families) and 27 monophagous species (feeding only on one plant genus). For three species (*Utecha trivia*, *Megophthalmus scabripennis* and *Megamelodes quadrimaculatus*) the host plants are still uncertain. Seven of the species have been classified by the 'Biological Records Centre' (BRC) or in Kirby (1992) as 'notable', which means they are thought to be nationally scarce and occupy fewer than 100 10×10 km cells of the UK National Grid.

Altogether 14 chalk grassland species, 29 dry grassland species, 21 eurytopic species and 10 nitrophilic species were sampled during the project (Table 5). The number of recorded species per site varied from just six up to a maximum of 39 recorded species on the richest site. On average, a site contained 20 Auchenorrhyncha species. There were at least one nitrophilic or four eurytopic species recorded from every site. On the other hand, some sites lack typical dry grassland or chalk grassland species completely.

Comparison of Auchenorrhyncha assemblages linked to NVC vegetation communities

As with the composition of vegetation, differences in Auchenorrhyncha assemblages are most distinct at the highest hierarchical levels of community classification. In this study this reflects the comparison of calcicolous grasslands (CG) with mesotrophic grasslands (MG), the two major grassland types occurring on chalk soils in southern England. On the CG sites, 89 leafhopper species could be found in comparison to only 76 species on the MG sites. The maximum number of species found on a single CG site is not much higher than the value found on the most diverse of the MG sites (Table 6). However, the average number of species for the CG sites is significantly higher than the value for the MG sites. The average number of typical chalk grassland species is highly significantly different between the two grassland groups, with more than four on CG sites compared with only two on the MG sites. The same applies for dry grassland species, where the number of typical dry grassland leafhoppers is nearly double the number occurring on the MG sites (Table 6). On the other hand, the average number of nitrophilic species is significantly higher on MG sites compared with the CG sites (Table 6).

All constant species show a significant preference for one of the two groups (Table 7). Of the eight species occurring in both groups with a frequency of class IV or V, three appear in

Table 5. Auchenorrhyncha species classified in order of their indicator qualities for Great Britain.

Chalk grassland species	Dry grassland species	Eurytopic species	Nitrophilic species
Kelisia occirrega	*Kelisia occirrega*	*Criomorphus albomarginatus*	*Javesella pellucida*
Kelisia guttula	*Eurysanoides douglasi*	*Dicranotropis hamata*	*Aphrodes makarovi*
Eurysanoides douglasi	*Ribautodelphax pungens*	*Javesella dubia*	*Anoscopus serratulae*
Ribautodelphax pungens	*Utecha trivia*	*Javesella pellucida*	*Eupteryx urticae*
Utecha trivia	*Batracomorphus irroratus*	*Philaenus spumarius*	*Deltocephalus pulicaris*
Batracomorphus irroratus	*Emelyanoviana mollicula*	*Megophthalmus scanicus*	*Cicadula persimilis*
Emelyanoviana mollicula	*Mocydia crocea*	*Aphrodes makarovi*	*Euscelis incisus*
Eupteryx notata	*Mocydiopsis attenuata*	*Anoscopus albifrons*	*Euscelis lineolatus*
Arboridia parvula	*Psammotettix cephalotes*	*Anoscopus serratulae*	*Psammotettix confinis*
Mocydia crocea	*Adarrus multinotatus*	*Eupteryx aurata*	*Errastunus ocellaris*
Mocydiopsis attenuata	*Turrutus socialis*	*Zyginidia scutellaris*	
Psammotettix cephalotes	*Hyledelphax elegantula*	*Macrosteles laevis*	
Adarrus multinotatus	*Ribautodelphax angulosa*	*Deltocephalus pulicaris*	
Turrutus socialis	*Kosswigianella exigua*	*Doratura stylata*	
	Neophilaenus exclamationis	*Elymana sulphurella*	
	Anaceratagallia ribauti	*Athysanus argentarius*	
	Anaceratagallia venosa	*Euscelis incisus*	
	Eupelix cuspidata	*Streptanus aemulans*	
	Aphrodes bicincta	*Psammotettix confinis*	
	Arboridia parvula	*Jassargus pseudocellaris*	
	Eupteryx origani	*Arthaldeus pascuellus*	
	Zygina hyperici		
	Rhytistylus proceps		
	Rhopalopyx adumbrata		
	Arocephalus punctum		
	Doratura stylata		
	Jassargus pseudocellaris		
	Dikraneura variata		
	Psammotettix albomarginatus		

significantly higher abundance on the CG sites. These species, *Zyginidia scutellaris*, *Anoscopus albifrons* and *Kosswigianella exigua*, are therefore regarded as preferential species of this grassland type. On the other hand *Deltocephalus pulicaris*, *Euscelis incisus*, *Javesella pellucida*, *Arthaldeus pascuellus* and *Psammotettix confinis* are preferential species of mesotrophic grasslands. Of the 29 species characteristic of CG sites, only three are also frequent on MG sites, whereas of the 12 preferential species of the MG sites, five were also frequent on CG sites.

Utecha trivia, *Psammotettix cephalotes*, *Eurysanoides douglasi* and *Ribautodelphax pungens* are classified as differential species of calcicolous grassland, the latter two species because of the low frequency of their host grass *Brachypodium pinnatum* in mesotrophic grasslands (Table 7). There are no differential species of mesotrophic grasslands. The group of general associates comprises 53 species. About 19 of them have been found exclusively on CG sites, seven only on MG sites.

Of the six notable species recorded in the samples, four (*Agallia brachyptera*, *Utecha trivia*, *Eurysanoides douglasi*, *Ribautodelphax pungens*) have been found only on calcicolous grassland. With the exception of *Agallia brachyptera*, which could not be found in a sufficient frequency or abundance, all of them can be classified as differential species. *Psammotettix albomarginatus* and *Ribautodelphax angulosa*, both 'notable B' species, each was found exclusively on a single site, both belonging to mesotrophic grassland. Again, both species were not found in sufficient abundance to classify them as differential species.

A comparison of the regularly managed CG2 grassland with the ranker calcicolous grasslands (CG3–5) displays ten constant species, which occur with high frequency and abundance in both grassland types (Table 8). Of these, only *Zyginidia scutellaris* can be considered a dominant species in both grassland groups, becoming sometimes an eudominant species. The nine preferential species of the CG2 grassland,

Table 6. Average numbers of individuals and species recorded per site with S.E. of the mean.

	Comparison CG v. MG grassland		Comparison CG2 v. CG3–5 grassland		Comparison of CG sub-communities		
	CG (n = 52)	MG (n = 29)	CG2 (n = 37)	CG3–5 (n = 15)	CG2a (n = 14)	CG2b (n = 7)	CG2c (n = 16)
Auchenorrhyncha specimens (excl. larvae)	332 ± 19.9	412.7 ± 42.2	309 ± 22.8	387.8* ± 37.4	313.5 ± 26.7	376 ± 65.2	275.8 ± 37.3
Auchenorrhyncha specimens (incl. larvae)	1274 ± 104	1264 ± 107	1341.1 ± 129	1106.7 ± 164	1154.1 ± 185	1703 ± 288	1346.4 ± 217
Auchenorrhyncha species per site	22.2* ± 0.9	18.1 ± 1.4	21.6 ± 1.2	23.7 ± 1.3	23.8 ± 1.9	21.7 ± 2.3	19.6 ± 1.9
Chalk grassland species per site	4.3** ± 0.3	1.7 ± 0.3	3.9 ± 0.4	5.3 ± 0.6	5.1[a] ± 0.6	5.1[a] ± 0.6	2.4[b] ± 0.3
Dry grassland species per site	7.7** ± 0.4	3.9 ± 0.6	7.3 ± 0.5	8.7 ± 0.7	9.4[a] ± 0.9	8.9[a] ± 0.9	4.9[b] ± 0.5
Eurytopic species per site	9.0 ± 0.4	9.6 ± 0.5	8.9 ± 0.5	9.0 ± 0.8	8.9 ± 0.7	8.0 ± 0.8	9.5 ± 0.9
Nitrophilic species per site	4.1 ± 0.3	5.7** ± 0.2	4.1 ± 0.3	4.0 ± 0.5	3.9 ± 0.5	4.0 ± 0.7	4.4 ± 0.5
Plant species per site	41.7** ± 1.9	32.4 ± 1.8	41.2 ± 2.3	42.9 ± 3.2	38.2 ± 4.7	38.9 ± 2.7	44.4 ± 2.1
Grass species per site	13.2* ± 0.6	11.0 ± 0.5	13.7* ± 0.8	12.1 ± 0.9	13.4 ± 1.8	12.4 ± 1.3	14.5 ± 0.6
Average plant diversity (H_s)	2.2** ± 0.05	1.9 ± 0.08	2.2 ± 0.05	2.2 ± 0.09	2.2 ± 0.09	2.2 ± 0.19	2.2 ± 0.06

Significance of difference in average abundance tested with Mann–Whitney U; * = $p \leq 0.05$, ** = $p \leq 0.001$; values with different letters = $p \leq 0.05$; values with the same letter or without letters are not significantly different.

particularly *Kosswigianella exigua* and *Neophilaenus exclamationis*, are species known to prefer short swards. Interestingly, *Euscelis incisus*, *Arthaldeus pascuellus*, *Psammotettix confinis*, above preferential species of the MG grassland, reappear here now as preferential species of the CG2 grassland community.

Although showing a lower total number of recorded species, probably the result of a lower level of replication, the number of preferential species is, at 13, notably higher on the CG3–5 grassland. This group comprises species known to prefer tall grass stands like *Neophilaenus lineatus*, *Mocydia crocea*, *Stenocranus minutus*, *Criomorphus albomarginatus* and *Rhytistylus proceps*. In addition, *Kelisia occirrega*, although living on the short growing sedge *Carex flacca*, which occurs in higher abundances on the CG2 grassland (Rodwell 1992), is a valuable preferential species of the ranker chalk grassland communities.

Delphacinus mesomelas and *Utecha trivia* can both be classified as CG2 differential species in comparison with the CG3–5 grassland. The only differential species of the CG3–5 grassland is *Eurysanoides douglasi*, suggesting that its occurrence may be restricted to dense undisturbed growing patches of its only host plant *Brachypodium pinnatum*. It is noteworthy that, despite no significant differences in species richness, the average abundance of leafhoppers is significantly higher on the ranker chalk grassland communities.

The comparison of three sub-communities within the CG2 grassland show very similar results for the botanical parameters (Table 6). The number of Auchenorrhyncha species is highest on CG2a, though not significantly in comparison with the other two sub-communities. Numbers of typical chalk grassland and dry grassland species are significantly lower on CG2c grassland in contrast to CG2a and CG2b, consistent with the occurrence of this sub-community on damper and more fertile chalk soils (Table 6).

Altogether 15 leafhopper species can be classified as constants, occurring in a high frequency class in at least two of the three CG2 sub-communities for which comparisons are possible in this study (Table 9). However, there is evidence for habitat preferences for some species visible within this group. *Turrutus socialis* and *Eupelix cuspidata* are scarcer in CG2c grassland. On the other hand *Deltocephalus pulicaris* and *Psammotettix confinis* have their main occurrence on this sub-community. Altogether eight species can be classified as preferential species of CG2a grassland. In particular, *Kelisia occirrega* and *Arboridia parvula* seem to have the greatest affinities towards this sub-community. Four species are most frequent and abundant on the CG2b grassland. *Anoscopus serratulae* and *Streptanus sordidus*, both

Table 7. Comparison CG and MG grassland.

	CG			MG		
	Frequency	Dominance		Frequency	Dominance	
	$n = 52$	Average	Maximum	$n = 29$	Average	Maximum
Preferential species of CG						
Zyginidia scutellaris	V	5**	6	V	4	6
Anoscopus albifrons	V	4**	5	IV	2	4
Turrutus socialis	V	4**	6	II	1	3
Aphrodes makarovi	V	3	4	III	3	5
Kosswigianella exigua	IV	4*	6	IV	2	4
Hyledelphax elegantula	IV	4*	6	III	3	6
Eupteryx notata	IV	4**	6	III	2	4
Stenocranus minutus	IV	3	5	III	2	4
Neophilaenus lineatus	IV	3*	5	III	1	4
Philaenus spumarius	IV	3	4	III	2	4
Megophthalmus scanicus	IV	3	5	III	2	5
Mocydia crocea	IV	4**	6	II	2	5
Kelisia occirrega	IV	3**	5	II	1	4
Eupelix cuspidata	IV	3**	6	II	1	3
Neophilaenus exclamationis	III	4*	6	II	1	3
Recilia coronifer	III	2	4	II	3	5
Mocydiopsis attenuata	III	2	4	II	2	4
Criomorphus albomarginatus	III	2	4	II	1	4
Aphrodes bicincta	III	2*	4	II	1	2
Kelisia guttula	III	2**	4	I	1	3
Megophthalmus scabripennis	III	2*	5	I	1	3
Batracomorphus irroratus	II	3*	6	I	1	2
Psammotettix cephalotes	II	2*	4			
Delphacinus mesomelas	II	2*	3	I	1	4
Dikraneura variata	II	2	4	I	1	1
Agallia consobrina	II	1	4	I	1	1
Anaceratagallia venosa	II	1*	3	I	1	1
Utecha trivia	I	2	5	–	0	0
Eurysanoides douglasi	I	1	4	–	0	0
Ribautodelphax pungens	I	1	2	–	0	0
Preferential species of MG						
Deltocephalus pulicaris	IV	4	6	V	6**	6
Euscelis incisus	IV	3	5	V	4	6
Javesella pellucida	V	2	4	V	4**	5
Arthaldeus pascuellus	IV	2	4	V	4*	6
Psammotettix confinis	IV	3	6	V	4**	5
Euscelis lineolatus	II	2	5	IV	3**	6
Anoscopus serratulae	III	3	5	IV	3*	5
Streptanus sordidus	III	2	4	IV	3*	5
Macrosteles viridigriseus	II	1	4	III	3	5
Psammotettix helvolus	I	1	3	II	3*	5
Muellerianella fairmairei	I	1	4	II	2	5
Xanthodelphax straminea	I	1	3	II	2	4
Conosanus obsoletus	I	1	3	II	2*	4
Associates						
Arboridia parvula	III	4	6	III	4	6
Anaceratagallia ribauti	III	3	5	III	4	6
Javesella dubia	III	2	4	III	3	5
Macrosteles laevis	II	2	5	II	2	4
Emelyanoviana mollicula	II	2	5	II	1	3
Doratura stylata	II	2	4	II	1	3

Table 7. (Continued).

	CG			MG		
	Frequency	Dominance		Frequency	Dominance	
	$n = 52$	Average	Maximum	$n = 29$	Average	Maximum
Rhytistylus proceps	II	2	4	II	1	3
Arthaldeus striifrons	II	1	4	I	1	2
Streptanus aemulans	II	1	3	II	2	4
Dicranotropis hamata	II	1	3	II	1	4
Anoscopus flavostriatus	II	1	3	II	1	3
Aphrophora alni	II	1	2	II	1	2
Rhopalopyx adumbrata	II	1	3	I	1	3
Elymana sulphurella	I	1	3	II	1	2
Eupteryx origani	I	1	3	I	1	4
Eupteryx urticae	I	1	2	II	1	3
Eupteryx vittata	I	1	3	I	1	2
Thamnotettix dilutior	I	1	3	I	1	2
Centrotus cornutus	I	1	2	I	1	2
Eurysa lineata	I	1	2	I	1	1
Evacanthus interruptus	I	1	2	I	1	1
Graphocraerus ventralis	I	1	2	I	1	1
Cicadula persimilis	I	1	2	I	1	1
Adarrus multinotatus	I	1	2	I	1	1
Eupteryx aurata	I	1	1	I	1	2
Eupteryx stachydearum	I	1	1	I	1	1
Allygus mixtus	I	1	1	I	1	1
Agallia brachyptera	I	1	3			
Evacanthus acuminatus	I	1	3			
Jassargus flori	I	1	3			
Tachycixius pilosus	I	1	2			
Planaphrodes bifasciata	I	1	2			
Cicadella viridis	I	1	2			
Notus flavipennis	I	1	2			
Fagocyba cruenta	I	1	2			
Alnetoidea alneti	I	1	2			
Balclutha punctata	I	1	2			
Speudotettix subfusculus	I	1	2			
Athysanus argentarius	I	1	2			
Macustus grisescens	I	1	2			
Arocephalus punctum	I	1	2			
Jassargus pseudocellaris	I	1	2			
Forcipata citrinella	I	1	1			
Edwardsiana crataegi	I	1	1			
Zygina flammigera	I	1	1			
Allygus modestus	I	1	1			
Macropsis fuscula				I	1	3
Megamelodes quadrimaculatus				I	1	2
Ribautodelphax angulosa				I	1	2
Psammotettix albomarginatus				I	1	2
Errastunus ocellaris				I	1	2
Ribautiana tenerrima				I	1	1
Zygina hyperici				I	1	1

Significance of difference in average abundance tested with Mann–Whitney U; * = $p \leq 0.05$, ** = $p \leq 0.001$; column 'maximum' refers to the highest dominance class a species reaches on at least one of the investigated sites.

Table 8. Comparison CG2 and the combined samples of CG3, CG4 and CG5 grassland (excl. associates).

	CG2			CG3–5		
	Frequency	Dominance		Frequency	Dominance	
	$n = 37$	Average	Maximum	$n = 15$	Average	Maximum
Constant species						
Zyginidia scutellaris	V	5	6	V	5	6
Anoscopus albifrons	V	4	5	V	4	5
Turrutus socialis	V	4	5	V	5	6
Aphrodes makarovi	V	3	4	V	3	4
Javesella pellucida	V	2	4	V	3	4
Eupteryx notata	V	4	6	IV	3	5
Deltocephalus pulicaris	V	4	6	IV	4	6
Eupelix cuspidata	IV	3	5	V	4	6
Hyledelphax elegantula	IV	4	6	IV	3	5
Megophthalmus scanicus	IV	3	5	IV	2	3
Preferential species of CG2						
Kosswigianella exigua	V	4*	6	III	4	6
Euscelis incisus	V	4*	5	III	3	5
Psammotettix confinis	IV	3	6	III	2	4
Arthaldeus pascuellus	IV	3	4	III	2	4
Neophilaenus exclamationis	III	4*	6	II	2	5
Megophthalmus scabripennis	III	3	5	II	1	3
Javesella dubia	III	2	4	II	2	4
Delphacinus mesomelas	III	2*	3			
Utecha trivia	II	2	5			
Psammotettix cephalotes	II	2	4	I	1	1
Preferential species of CG3–5						
Neophilaenus lineatus	IV	3	5	V	3*	4
Mocydia crocea	III	3	6	V	4**	5
Kelisia occirrega	III	3	5	V	4*	5
Stenocranus minutus	III	3	5	V	3*	5
Anaceratagallia ribauti	III	3	5	IV	3*	4
Philaenus spumarius	III	2	4	IV	3	4
Aphrodes bicincta	III	2	4	IV	2	3
Mocydiopsis attenuata	II	2	4	IV	2	4
Criomorphus albomarginatus	II	1	4	IV	2*	4
Rhytistylus proceps	II	1	4	III	3*	4
Recilia coronifer	II	2	4	III	2	4
Arthaldeus striifrons	II	1	3	III	2	4
Eurysanoides douglasi				II	2*	4

Significance of difference in average abundance tested with Mann–Whitney U; * = $p \leq 0.05$, ** = $p \leq 0.001$; column 'maximum' refers to the highest dominance class a species reaches on at least one of the investigated sites.

preferential species of the broad mesotrophic grassland type (see above), typically have their main distribution within the CG2 grassland sub-community associated with the more mesotrophic conditions (*Holcus lanatus–Trifolium repens* sub-community, CG2c). Also noteworthy is the significant absence of characteristic chalk grassland species like *Batracomorphus irroratus* and *Utecha trivia* from the CG2c sub-community. No differential species can be identified at the sub-community level within CG2 grasslands.

Discussion

Correlation between Auchenorrhyncha assemblages and NVC communities

Morris (1990) demonstrated that chalk grassland sites can differ greatly in their Auchenorrhyncha species composition. Even in relatively stable old grasslands, the leafhopper assemblages of sites with known history and management can be predicted only to a certain degree (Brown et al. 1992). On the

Table 9. Comparison of the CG2a, CG2b and CG2c sub-communities (excl. associates).

	CG2a			CG2b			CG2c		
	Frequency	Dominance		Frequency	Dominance		Frequency	Dominance	
	$n = 14$	Average	Maximum	$n = 7$	Average	Maximum	$n = 16$	Average	Maximum
Constant species									
Anoscopus albifrons	V	4	5	V	3	4	V	3	5
Zyginidia scutellaris	V	5	6	V	5	6	V	5	6
Javesella pellucida	V	2	3	V	2	3	IV	2	4
Kosswigianella exigua	V	4^{a}	6	V	5^{b}	5	IV	4^{a}	5
Turrutus socialis	V	4^{ab}	5	V	5^{a}	5	IV	3^{b}	4
Aphrodes makarovi	V	3	4	V	2	3	III	3	4
Eupelix cuspidata	V	3^{a}	4	V	4^{a}	5	II	2^{b}	4
Euscelis incisus	V	3^{a}	4	IV	4^{ab}	5	V	4^{b}	5
Hyledelphax elegantula	V	4	5	IV	4	5	IV	4	6
Deltocephalus pulicaris	IV	3^{a}	4	V	3^{ab}	4	V	5^{b}	6
Eupteryx notata	IV	4	6	V	4	6	IV	4	6
Megophthalmus scanicus	IV	2	3	IV	2	3	IV	3	5
Arthaldeus pascuellus	IV	2	4	III	2	3	IV	3	4
Neophilaenus lineatus	III	3	5	V	2	3	IV	3	4
Psammotettix confinis	III	3	4	V	2	3	IV	4	6
Preferential species of CG2a									
Kelisia occirrega	V	3^{a}	5	IV	3^{ab}	4	II	2^{b}	4
Arboridia parvula	IV	4^{a}	6	III	3^{b}	5	II	3^{ab}	5
Philaenus spumarius	IV	3	4	II	1	3	III	3	4
Mocydia crocea	IV	4	6	II	3	4	III	2	4
Mocydiopsis attenuata	III	2	4	II	1	3	II	2	4
Dikraneura variata	III	2	4	II	2	3	I	2	4
Psammotettix cephalotes	III	2^{a}	4		^{b}			^{ab}	
Aphrophora alni	III	1^{a}	2		^{b}		I	1^{b}	2
Preferential species of CG2b									
Aphrodes bicincta	III	1^{a}	3	V	3^{b}	4	III	1^{ab}	3
Kelisia guttula	III	1^{ab}	3	V	2^{a}	4	II	1^{b}	3
Neophilaenus exclamationis	II	4^{a}	5	V	4^{b}	5	III	4^{ab}	6
Batracomorphus irroratus	II	3^{a}	5	IV	1^{a}	3		^{b}	
Preferential species of CG2c									
Anoscopus serratulae	III	3	5	II	2	3	IV	3	4
Javesella dubia	II	1^{ab}	3	II	1^{a}	2	IV	2^{b}	4
Streptanus sordidus	II	2^{a}	4	II	1^{a}	2	IV	2^{b}	4
Delphacinus mesomelas	II	1	3	II	1	3	III	2	3
Criomorphus albomarginatus	II	2	4				III	2	4
Macrosteles viridigriseus	I	1	2	II	1	1	III	2	4

Significance of difference in average abundance tested with Mann–Whitney U; $p \leq 0.05$, values with the same letter or without letters are not significantly different; column 'maximum' refers to the highest dominance class a species reaches on at least one of the investigated sites.

other hand, in spite of the unique characteristics of individual sites, the use of large-scale projects involving many sampling sites should allow the description of the general pattern of occurrence and preferences of individual species. This is likely to be the case for Auchenorrhyncha, since the correlation between vegetation composition and herbivore groups is expected to be much tighter than between vegetation and predatory groups such as ground beetles or spiders (Irmler et al. 1998). It is therefore surprising, that there have been no previous attempts to link Auchenorrhyncha assemblages (and few considering other insects) to NVC units, and only few relating leafhopper assemblages with a more broader habitat classification and successional stages (Hollier et al. 1994; Eyre et al. 2001; Hamilton 2005). Comparable studies and classification schemes conducted on the European continent concentrated on different grassland types and are not comparable with the situation in Britain (e.g., Marchand 1953; Remane 1958). In Britain, only recently has there been an attempt to relate insect assemblages to NVC plant communities, in this case using carabid beetles (Blake et al. 2003). This follows earlier attempts to classify grassland habitats on a broader British and European scale using carabid beetles (Eyre and Luff 1990; Luff et al. 1992).

This study demonstrates that different vegetation communities are reflected by distinct Auchenorrhyncha assemblages. Significant differences were observed down to the level of sub-communities. The resulting simple NVC-listings of leafhoppers substantially broaden our knowledge on the diversity and community composition of the investigated habitat types. Additionally, they allow a much better understanding of the ecology of many constituent species, by showing their habitat preferences. How important such knowledge can be was only recently demonstrated by using leafhoppers linked to prairie communities to reconstruct the historic distribution of a long lost habitat (Hamilton 2005). Our data gives evidence that some leafhopper species probably have different niches within calcareous grassland than previously thought. *Aphrodes makarovi* and *Eupelix cuspidata*, widely distributed and on average highly abundant species in chalk grasslands, were previously under-recorded. *Anoscopus albifrons*, so far only observed in one study as a dominant species on calcareous grassland, turned out to be one of the most frequent and dominant species in this study. Morris (1971) considered *Recilia coronifer*, *Agallia consobrina*, *Anoscopus flavostriatus* and *Hyledelphax elegantulus* to be species of casual occurrence on calcicolous grassland, but all of these species were found regularly on unimproved chalk grassland in this study, suggesting that they form a substantial part of the Auchenorrhyncha fauna on British calcicolous grassland.

On the other hand, some of the abundant species from previous studies on calcareous grassland (Morris 1971, 1973, 1990; Cook 1996) were absent or found in extremely low numbers during the presented study. These species, namely *Forcipata citrinella*, *Neophilaenus campestris*, *Arocephalus punctum* and *Planaphrodes bifasciatus* seem to be of less importance as typical components of calcareous grassland than one would assume from previous studies. However, this may either apply only to the geographical regions investigated here, or indicate differences in invertebrate assemblages between chalk and harder limestone substrates. It is important to point out the regional differences occurring in Auchenorrhyncha communities similar to the regional differences of vegetation assemblages. According to Cook (1996) *Adarrus multinotatus*, *Planaphrodes bifasciatus*, *Turrutus socialis* and *Verdanus abdominalis* were the most abundant leafhoppers on calcareous grassland in northern England. Only *T. socialis* is also a common and characteristic calcareous grassland species on chalk in southern England; *Verdanus abdominalis* was completely absent and the other two species extremely rare.

The role of preferential species

At a higher community level, here reflected in the comparison of chalk grasslands with agriculturally improved mesotrophic grasslands, leafhopper assemblages basically reflect conditions more readily apparent through vegetation data, indicating a congruent response of plants and insects to agricultural improvement. Plant and leafhopper species richness, plant diversity and the richness of highly specialised leafhoppers indicate equally the important role of unimproved chalk grassland within regional or national biodiversity, in contrast to degraded communities on improved grassland, as has been repeatedly demonstrated both for vegetation and invertebrate communities (e.g., Smith 1980; Ruesink 1995; Carvell 2002). This supports the idea that, at least on the level of a broader habitat classification, insect conservation management might work sufficiently well through approaches based purely on a knowledge of vegetation type (Panzer and Schwartz 1998).

However, our results suggest that linking insect assemblages to vegetation classifications can be of importance when lower levels of plant community organisation are taken into account, where differences in botanical structure and species composition are small. Here preferential invertebrate species are able to provide additional information often required for the evaluation of conservation priorities. Plant species richness and diversity is similar when well-managed downland (CG2) is compared with ranker, less intensively managed, communities (CG3–5). The number of Auchenorrhyncha species is not significantly different, but shows a trend towards higher numbers within the ranker communities. This is not surprising considering the preference of a high number of Auchenorrhyncha and other insect species for tall vegetation and sites with a low amount of disturbance (Andrzejewska 1965, 1979, 1991; Morris 1981a, b, 2000; Cherrill and Brown 1990). Of the seven notable Auchenorrhyncha species recorded, four (*Eurysanoides douglasi*, *Ribautodelphax angulosa*, *Ribautodelphax pungens*, *Athysanus argentarius)* prefer taller swards and one is typical of rank but open vegetation (*Agallia brachyptera*) (Kirby 1992; Schiemenz et al. 1996; Nickel 2003). Only *Utecha trivia* shows a slight preference for short turf (Morris 1971; Kirby 1992). Increases in leafhopper species richness after cessation of grazing supports the importance of insects as biological indicators particularly when the composition of vegetation does not react significantly. This has been recently demonstrated for grassland through a study using a range of insect orders including Auchenorrhyncha (Kruess and Tscharntke 2002). Most important however, is the difference in the Auchenorrhyncha species composition; both types of grasslands compared here are the preferred habitats of a number of chalk or at least dry grassland specialists and are exclusively inhabited by specialised preferential and differential species.

The importance of single species as biological indicators become particularly obvious through the preferential species of CG3–5 grassland. Cessation of management on chalk grassland originally belonging to CG2 tends to result in successional stages dominated by *Brachypodium pinnatum* and/or *Bromopsis erecta* leading to CG3–5. The later group of communities is generally regarded as a degraded stage of managed chalk grassland and is often inferior to the former one in terms of species diversity (Kirby 2001). Hurst and John (1999) demonstrated the detrimental effect of *Brachypodium pinnatum* on plant species richness. However, some of the rarest insect species in Britain, namely *Eurysanoides douglasi* and *Ribautodelphax pungens*, rely on extensive areas of *B. pinnatum*. Equally, *Kelisia occirrega*, a species feeding on *Carex flacca*, a low-growing sedge that occurs in higher abundance on CG2 grassland compared to CG3–5, prefers the latter habitat indicating that it is especially sensitive to disturbance. Such a preference for unmanaged sites by a number of insects as has been previously suggested for a number of insects (Kruess and Tscharntke 2002).

The differences in botanical species composition and vegetation structure at the level of sub-communities are even less prominent. The CG2b sub-community differs from the classical chalk downland CG2a sub-community as a result of slightly higher soil fertility, with generally a higher plant species richness. CG2c grassland is characterised by even more fertile conditions, with plants typical of mesotrophic grassland communities becoming more dominant. In contrast, the differences in the Auchenorrhyncha assemblages are quite remarkable despite the similarity of the botanical assemblages. Firstly, the high number of leafhopper species on CG2a grassland in comparison with CG2c is notable. In this respect CG2c shows its closeness to comparably species poor mesotrophic grassland. Further, the richness of typical chalk grassland and dry grassland Auchenorrhyncha is higher on the CG2a and CG2b grassland compared with the CG2c. Additionally, the average number of eurytopic and nitrophilic species is highest within the CG2c sub-community. In summary these results indicate a higher importance of CG2a and CG2b for the conservation of insect biodiversity in comparison to CG2c grassland, which could not be demonstrated in this study through the vegetation data via species richness or plant diversity.

It is notable, that particularly uncommon or rare species often show a strong preference for one of the compared communities, as *Neophilaenus exclamationis*, *Delphacinus mesomelas* and *Utecha trivia* do for CG2 or, in contrast *Eurysanoides douglasi* for CG3–5. This is of high importance for species conservation since community analyses based purely on the similarities between assemblages often have to neglect uncommon species for methodological reasons (for example Blake et al. 2003).

Target species

It is not always the most diverse site or the habitat with the highest insect density that is most important to conserve. It is clearly the case that species poor habitats can contribute substantially to the overall diversity on a landscape, regional or even national scale if they contain highly specialised taxa. Within British calcicolous grassland some extremely rare leafhopper species like *E. douglasi* and *R. pungens* are restricted to habitats of relatively low plant species richness, as shown above. The same may be true for *Euscelis venosus*, a very rare species in England known only from rank sites on chalk (Kirby 1992). *Kelisia occirrega*, in spite of an apparently relatively wide distribution on British calcicolous grassland in this study, may equally deserve a high conservation priority due to its very restricted range, with additional records known only from western France and Spain (Remane and Guglielmino 2002). Conservation of such species has to be targeted through separate measures since they are not protected through management based purely on consideration of vegetation type. In fact such measures may actively endanger these species in some cases.

Although the conservation status of a site is usually indicated through the floristic composition, a further group of species allows a more detailed habitat evaluation, of particular use when conservation priorities have to be set among sites of similar vegetation. These species may also serve as indicators for the occurrence of subtle differences in vegetation structure, microclimate, etc., which are beneficial for a range of other invertebrates more difficult to survey or of unknown ecology. Our data suggest that *Utecha trivia*, *Psammotettix cephalotes* and *Batracomorphus irroratus* in particular are sufficiently rare and highly specialised to well managed chalk grassland to belong to this group. Additionally, *Anakelisia perspicillata*, *Hephathus nanus* and to a certain degree *Tettigometra impressopunctata*, all species which are extremely rare, should also included into this group according to their preference for calcicolous grassland within the UK (Kirby 1992).

Finally, a group of more widely distributed preferential species of calcicolous grassland identified in this study, like *Turrutus socialis*, *Mocydiopsis attenuata* and *Kelisia guttula*, may turn out to be suitable indicators to measure the success of restoration management, particularly in cases where botanical data already seem to show early success.

Conclusions

The method of data presentation utilised in this study allows a quick but detailed overview of the investigated invertebrate assemblages, and can be used as a practical method to recognise important habitat preferences of species important for conservation. It is particularly suited to guard against the setting of inappropriate management prescriptions, which can otherwise arise when only basic community parameters such as species richness or purely vegetation-based approaches are chosen to set priorities for habitat conservation. Preferential and differential species, as described here, are useful biological indicators to make intelligible the subtle differences between NVC plant communities. These species can also be considered as suitable indicators to measure success or failure of long term grassland restoration.

Despite the limitations of this study in terms of coverage, the data presented could already be useful for conservation. For example, the success of habitat restoration on chalk in southern England could be assessed by monitoring the Auchenorrhyncha communities and comparing the results with the average assemblage of the target grasslands. Displaying faunistical data in this way allows comparison of the insect fauna of different grassland types, but it should be possible to use this method more generally with other types of habitat classification. In the same way that use of the NVC has been developed over the years since its introduction, invertebrate data from further studies can easily be incorporated into the system for which an initial basic framework is provided here.

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