Responses of invertebrate trophic level, feeding guild and body size to the management of improved grassland field margins

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Summary

1. Management of lowland mesotrophic grasslands in north-west Europe often makes use of inorganic fertilizers, high stocking densities and silage-based forage systems to maximize productivity. The impact of these practices has resulted in a simplification of the plant community combined with wide-scale declines in the species richness of grassland invertebrates. We aim to identify how field margin management can be used to promote invertebrate diversity across a suite of functionally diverse taxa (beetles, planthoppers, true bugs, butterflies, bumblebees and spiders).

2. Using an information theoretic approach we identify the impacts of management (cattle grazing, cutting and inorganic fertilizer) and plant community composition (forb species richness, grass species richness and sward architecture) on invertebrate species richness and body size. As many of these management practices are common to grassland systems throughout the world, understanding invertebrate responses to them is important for the maintenance of biodiversity.

3. Sward architecture was identified as the primary factor promoting increased species richness of both predatory and phytophagous trophic levels, as well as being positively correlated with mean body size. In all cases phytophagous invertebrate species richness was positively correlated with measures of plant species richness.

4. The direct effects of management practices appear to be comparatively weak, suggesting that their impacts are indirect and mediated though the continuous measures of plant community structure, such as sward architecture or plant species richness.

5. *Synthesis and applications.* By partitioning field margins from the remainder of the field, economically viable intensive grassland management can be combined with extensive management aimed at promoting native biodiversity. The absence of inorganic fertilizer, combined with a reduction in the intensity of both cutting and grazing regimes, promotes floral species richness and sward architectural complexity. By increasing sward architecture the total biomass of invertebrates also increased (by *c*. 60% across the range of sward architectural measures seen in this study), increasing food available for higher trophic levels, such as birds and mammals.

Key-words: cutting, NPK fertilizer, phytophagous, plant species richness, pollinators, predatory, sward architecture

Introduction

Across north-west Europe, lowland mesotrophic grasslands have increasingly been managed to maximize productivity by increasing stocking density and yields of standing or stored

grass products (Blackstock *et al.* 1999; Frame 2000; Hodgson *et al.* 2005). These intensive management practices include the application of inorganic fertilizers (NPK), re-seeding, improved drainage and the replacement of hay with silage cutting as the principal conserved forage (Frame 2000). As a result 'improved' grasslands are floristically species poor and structurally uniform (Vickery *et al.* 2001). For this reason they typi-

cally have a low biodiversity value, not only for plants, but also for invertebrates and birds (Blackstock *et al.* 1999; Vickery *et al.* 2001; Hutton & Giller 2003; Woodcock *et al.* 2007a). In addition, intensively managed grasslands have typically replaced traditionally managed, high conservation value pasture, while economic factors have also driven the wide-scale replacement of grasslands by arable agriculture (Blackstock *et al.* 1999; Haines-Young *et al.* 2003).

While the restoration of traditionally managed semi-natural pastures or hay meadows can increase biodiversity, the wide-scale uptake of such approaches has economic limitations (Abensperg-Traun *et al.* 2004). One alternative is to enhance biodiversity using approaches that can be applied in combination with existing profitable farming management practices. By using alternative management in the field margin areas, an approach used extensively in arable agriculture (e.g. Marshall & Moonen 2002), this goal may be achievable in intensively managed grassland systems (Haysom *et al.* 2004; Woodcock *et al.* 2007a).

Invertebrates are an abundant and functionally important component of grasslands (Voigt, Perner & Jones 2007), supporting nutrient cycling (Hutton & Giller 2003) and pollination (Forup & Memmott 2005), while providing a link between plants and higher trophic levels, such as birds (Vickery *et al.* 2001). While it is widely acknowledged that intensive grassland management has negatively impacted on invertebrates, the data supporting this are limited in terms of the range of taxa considered (e.g. Hutton & Giller 2003; Haysom *et al.* 2004; Woodcock *et al.* 2007a). There is a need to understand how management within intensive grasslands can be used to enhance invertebrate diversity across a broad range of taxonomic groups, rather than focusing on select families or orders.

This study investigates how manipulating field margin management and plant composition can be used to benefit invertebrate diversity in intensive grasslands. We incorporate data on the true bugs (Heteroptera, Hemiptera), planthoppers (Auchenorrhyncha, Hemiptera), beetles (Coleoptera), bumblebees (Apidae, Hymenoptera), butterflies (Lepidoptera) and spiders (Araneae), with the aim of providing an overall perspective on how above-ground invertebrates respond to intensive grassland management. Rather than focusing on the responses of individual taxa, we consider their response in terms of trophic level, feeding guilds and gradients in body size, all of which cross conventional taxonomic groupings (Blondel 2003). An understanding of the functional responses and the impacts on plant community structure will allow us to predict the invertebrate response to management. Such an approach will therefore have wide applicability to the management of other grassland agro-ecosystems, beyond those considered here.

We make four predictions: (i) Increasing the architectural complexity of the sward will provide additional niche space for both phytophagous and predatory trophic levels, increasing their species richness; (ii) Phytophagous invertebrate species richness will be positively correlated with plant species richness; (iii) Management regimes associated with increased sward disturbance are expected to have negative impacts on invertebrate species richness. However, generalists (e.g. polyphagous plant feeders) will be less susceptible to disturbance than specialists (e.g. monophagous/oligophagous plant feeders) as their wide resource base will make them more resilient to the loss of specific resources; (iv) Management associated with increased disturbance will result in a reduction in mean body size across all invertebrates (Blake *et al.* 1994). Understanding how body size responds to gradients of disturbance will provide insights into the functionality of grassland invertebrate communities, particularly in relation to resource use and energy flow (Saint-Germain *et al.* 2007).

Materials and methods

STUDY SITE

The study was undertaken on four UK farms, two each in Somerset (Bickenhall, N50°58′47″: W2°59′29″; South Hill, N50°57′40″: W3°02′53″) and Devon (Heywoods, N50°48′38″: W3°55′40″; North Wyke, N50°46′14″: W3°55′46″). In each case sites were separated by at least 8 km. On-site stocking densities ranged from 4·0 to 5·5 cattle livestock units ha⁻¹, with inorganic fertilizer inputs typically around 360 kg nitrogen ha⁻¹, 20 kg phosphorus ha⁻¹ and 80 kg potassium ha⁻¹. All sites were dominated by species-poor *Lolium perenne* L. leys on clay loams.

Within each site a replicated block design experiment was established in 2003, with management prescriptions applied every year from 2003 to 2005 to create seven treatments. Treatments 1–7 were managed to create a gradient of increasing extensification of management practices. Individual experimental plots were 10×50 m and were fenced off from the remainder of the field, with each plot positioned so that the long edge was adjoining the field boundary. Prior to the start of the experiment the area covered by each experimental plot was managed in the same manner as the rest of the field, i.e. conventional intensive grassland management as described above. On each farm three replicates of the seven experimental treatments were established (a total of 84 plots across four farms, see Table 1). In summary, treatments 1–6 were cut to one of two heights (5 or 10 cm) in either May, July or on both dates. Treatments 1, 3 and 4 received NPK fertilizer, and treatments 1, 2 and 3 were grazed by cattle. Treatment 1 was representative of conventional intensive grassland management, being fertilized, cut in both May and July to a height of 5 cm and then aftermath grazed. Treatments 5–7 were the most extensively managed, receiving either single vegetation cut, or remaining effectively unmanaged throughout the study period (treatment 7). Further details on within-site conditions and existing habitat conditions can be found in Woodcock *et al.* (2007a).

VEGETATION SAMPLING

Each year the percentage cover of vascular plant species was visually estimated within five replicate 1×1 m (1 m²) quadrats arranged diagonally across each plot. Mean plant species richness for each experimental plot was determined from these quadrats for grasses and forbs. This distinction reflects common preferences of major grassland invertebrate taxa for either grasses (e.g. Auchenorrhyncha) or forbs (e.g. beetles) (e.g. Hoffman 1950–58; Biedermann & Niedringhaus 2004). The architectural complexity of the sward was assessed using vertical drop pins. Here sward architectural complexity is used to refer to the vertical distribution of plant structures throughout the sward. This method uses ten 3 mm diameter pins each 1 m in

Table 1. Summary of management practices used to establish the seven experimental field margin treatments

Management	Description	Treatments						
		1	2	3	4	5	6	7
Inorganic fertilizer application	A yearly application of 225 kg ha⁻¹ N, 22 kg ha⁻¹ P and 55 kg ha⁻¹ K, with the application split equally between two dates in March and April		*		*	*		
Cattle grazing	Aftermath cattle grazing following the July sward cut. Grazing was initiated at the start of September (c. 4·0–5·5 cattle livestock units ha⁻¹) until a sward height of 5–7 cm was reached		*	*	*			
Severe sward cut	Sward cut each year using conventional farm machinery to a height of 5 cm	May	*	*		*		
		July	*	*		*		*
Lenient sward cut	Sward cut each year using conventional farm machinery to a height of 10 cm	May				*		*
		July				*		
Annual number of sward cuts	Summed number of sward cuts in either May or July, independent of the height of the cut	2	2	2	2	1	1	0

height (separated by 10 cm) lowered vertically through the sward of each plot. The number of contacts of each vegetation category at 5 cm intervals up each pin was recorded. This provided detailed stratified information on the vertical distribution of grasses, forbs, legumes and dead vegetation. A modified version of the Shannon–Wiener diversity index was used to summarize information from the drop pin frames into a single parameter.

$$H_{Arch} = \sum_{i=1}^{n} p_i \log_e p_i$$

where H_{Arch} is the index of sward architectural complexity and p_i is the proportion of the total number of contacts with the drop pin in a particular plot at each height interval i. High H_{Arch} scores meant the sward had a high level of architectural complexity in terms of height and density of plant structures. Sward architecture was measured four times each year (April, June, July and September) for the years 2003–2005, from which an average yearly value was derived. While plant species richness and sward architecture measure different aspects of the plant community they are linked, there is a greater probability that in species-rich swards structurally complex plant species will be present (Woodcock *et al.* 2007b). However, sward architectural complexity, particularly in agricultural situations, is not simply a product of species, but is also the result of management effects, such as grazing, cutting and fertilizer applications. While the interpretation of sward architecture needs to be considered in the context of plant species richness, its effects on the invertebrate communities may potentially be quite different from those of plant species richness alone.

INVERTEBRATE SAMPLING

Standardized transect walks were used to measure the abundance and species richness of bumblebees and butterflies on each experimental plot following the methods described by Banaszak (1980) and Pollard & Yates (1993). Adult bumblebees and butterflies were recorded using a 50-m permanent transect running along the centre line of each plot, and extending 2·5 m either side of this line. For each sampling date (April, June, July and September) in each year transects were walked at a rate of 15–20 m min⁻¹, during which time bumblebees and butterflies were identified and recorded. Walks were carried out between 10.00 and 17.00 h, when weather conformed to Butterfly Monitoring Scheme standards (Pollard & Yates 1993), i.e. temperature > 13 °C with at least 60% clear sky, or 17 °C in any sky conditions, no rain, and wind speed < 5 on the Beaufort scale or 29–38 km h⁻¹. The six most common British bumblebees were recorded: *Bombus terrestris* (L.), *B. lucorum* L., *B. hortorum* (L.), *B. lapidarius* (L.), *B. pratorum* (L.) and *B. pascuorum* Scopoli); as *B. terrestris* and *B. lucorum* cannot be reliably distinguished in the field, workers of those species were recorded as an aggregate species (Prys-Jones & Corbet 1991). All adult butterflies were identified to species.

Adult beetles, true bugs, planthoppers and spiders were sampled using a Vortis suction sampler (Burkland Ltd, Rickmansworth, UK) during 2003, 2004 and 2005. In each year, samples were taken on dry days during April, June, July and September between 10.00 and 16.00 h. Both the June and September sampling rounds occurred 2 weeks after the sward cutting management had been applied. In each plot, 75 × 10 s suctions (0·26% of a plot's area) were taken for each sampling date. Suction sampling is a standard technique for the quantitative collection of grassland invertebrates (Brook *et al.* 2008). All true bugs, planthoppers and spiders were identified to species, as were beetles of the families Carabidae, Staphylinidae (excluding Aleocharinae), Chrysomelidae, Coccinellidae, Elateridae and Curculionoidea. The choice of which beetle families were identified was made on an *a priori* basis reflecting their dominance within improved mesotrophic grasslands (Woodcock *et al.* 2007a).

TROPHIC LEVEL, FEEDING GUILDS AND BODY SIZES

All invertebrates were assigned to either a predatory/polyphagous or obligate phytophagous trophic level. The predatory/polyphagous group included, in addition to obligate predators, those species which opportunistically consume plant matter. Hereafter, this tropic level is referred to as predatory. The phytophagous trophic level was split into feeding guilds according to whether host plants were from one genus (monophagous/oligophagous) or from many genera or

families (polyphagous). Designation to these trophic levels and feeding guilds was derived from existing published sources (e.g. Hoffman 1950–58; Southwood & Leston 1959; Roberts 1987; Prys-Jones & Corbet 1991; Biedermann & Niedringhaus 2004). Following Perner *et al.* (2005) larval feeding strategy was used to define feeding guild where this changed throughout the life cycle.

To reduce the effect of between-field variation in the location of different replicates (in terms of local soil conditions, moisture levels and historical field management) individual species abundance for the invertebrates was summed across these three replicates on each farm. Extrapolated species richness was estimated using the Chao unbiased estimator (Colwell & Coddington 1994) within the Vegan package of the R-statistical environment (R Development Core Team 2008). This was estimated separately for each of the trophic levels and feeding guilds from raw data matrices of species × experimental plots.

For each species a mean adult body length was also determined by measuring randomly chosen adults of five males and five females. The exception to this was for the bumblebees, where mean body length was derived from ten workers (all female). From this a weighted mean body length was then calculated for each experimental treatment at each site for the 3 years from 2003 to 2005 as:

$$\bar{x} = \frac{\sum_{i=1}^{n} L_i n_i}{\sum_{i=1}^{n} n_i}$$

where n_i is the density of the ith species and L_i is the mean body length of the ith species.

DATA ANALYSES

Values for each of the environmental variables (grass species richness, forb species richness and sward architecture) were averaged across the three replicate blocks of each farm. This corresponded with the approach described above for invertebrate species richness and mean body length. There was therefore a single value for treatments 1–7 for each farm, for each of the 3 years, for all continuous response and explanatory variables.

We did not use a conventional minimum adequate model approach to identify responses in trophic level species richness, guild species richness and weighted mean body length to field margin management and plant community structure. Instead, we employed an information theoretic approach to assess the impacts of management and plant community structure on the invertebrate assemblages (Burnham & Anderson 2002). The advantage of this approach is that it will identify which explanatory variables could affect the invertebrate communities, without being prone to the selection biases associated with conventional minimum adequate model methods of model simplification. Specifically, while parameter deletion may result in a single minimum adequate model, it would be likely that there would exist alternative models that were similar in their capacity to explain the data. This may be a product of inter-correlation within the explanatory variables and as a result of the process of model simplification, e.g. deletion or addition (Burnham & Anderson 2002). The information theoretic approach provides an unbiased method for estimating parameter importance by considering all potential model combinations. We outline the approach used in this analysis, although see Whittingham *et al.* (2006) for a comprehensive review.

Akaike's Information Criterion for small sample sizes (AIC_c) allows models with different numbers of parameters to be directly compared (Burnham & Anderson 2002). Applying this model selection approach, general linear mixed models (GLMM) in SAS 9.01 were used to assess responses of weighted mean body length, trophic level (predatory and polyphagous) and feeding guild (monophagous/oligophagous and polyphagous phytophagous) species richness to management and plant community structure. In all cases the fixed effects within the model were grazing (presence or absence), frequency of sward cuts (none, once or twice yearly), use of inorganic fertilizer (presence or absence), plant species richness (both forbs and grasses) and sward architecture. In all models, site was included as a random effect. The analysis focused on overall responses across all three years and so did not include year as a fixed effect, although year was included as a random effect to define the repeated measure structure of the data. Individual models were created for all combinations of the six fixed effects, ranging from the inclusion of single terms, up to and including all six parameters. For each of these models an AIC_c difference (Δ_i) was calculated as:

$$\Delta_i = AICc_i - AICc_{min}$$

where $AICc_{min}$ is the lowest recorded value for any model, and $AICc_i$ is the model-specific AIC_c value. Note this approach was undertaken separately for each of the response variables. The Δ_i indicates the relative support for each model, from which Akaike weights (w_i) (Burnham & Anderson 2002) were subsequently calculated as:

$$w_i = \frac{\exp\left[-\frac{1}{2}\Delta_i\right]}{\sum_{r=1}^{R} \exp\left[-\frac{1}{2}\Delta_r\right]}$$

where w_i represents the probability that model i would be selected as the best fitting model if the data were collected again under identical conditions. As the w_i of all R models sums to 1, this provides a basis for selecting a set of models for which there is a 95·0% confidence within which the most appropriate model for the data is contained. This is a variable selection approach which allows all models to be considered, while weighting them for their plausibility (Whittingham *et al.* 2006). Where multiple competing models exist (e.g. the models within the 95·0% confidence set) an approach is needed to provide estimates for the parameters (β) identified. To achieve this, parameter estimates for the explanatory variables were weighted by their Akaike weight and then averaged across all models (Burnham & Anderson 2002). This was done by using:

$$\beta_j = \sum_{i=1}^{R} w_i \beta_{j,i}^{+}$$

where w_i is the Akaike weight for model i and $\beta^{+}_{i,j}$ represents the estimate of β_i if parameter j is included in the model. Where parameter j is not included in the model β_i is set at zero.

Results

From 2003 to 2005 a total of 100 916 invertebrates were identified to species at the four sites. In order of decreasing contribution to this abundance (n) were the planthoppers ($n = 48\ 107$), beetles ($n = 33\ 102$), spiders ($n = 14\ 970$), true bugs ($n = 3932$), butterflies ($n = 672$) and bumblebees ($n = 133$). In terms of their contribution to total species richness (SR) this order differed, with the beetles being the most speciose (SR = 225), followed by the spiders (SR = 75), true bugs (SR = 59), planthoppers (SR = 47), butterflies (SR = 17) and bumblebees (SR = 5). Summary species

richness of the separate invertebrate taxa has been provided in Supporting Information Appendix S1.

TROPHIC LEVEL AND INVERTEBRATE SPECIES RICHNESS

For the predatory trophic level the information theoretic approach identified a 95·0% confidence set of three models (Table 2). All six fixed effects defining management (grazing, cutting and inorganic fertilizer) and the plant community composition (sward architecture, forb species richness and grass species richness) were present in at least two of these models. Mean parameter estimates of β suggest that sward architecture had the greatest overall effect, resulting in an increase in species richness of $c.$ 90·0% over the range of sward architecture values recorded (Fig. 1b). While grass species richness was positively correlated with predator species richness, there was a negative correlation with forb species richness (Fig. 2a,c). Disturbance in the form of aftermath grazing did result in a reduction in predator species richness (Fig. 3), which was not the case for either cutting or inorganic fertilizer application. The presence of both of these management practices resulted in small increases in species richness (< 6 species where the management was applied), while in the case of cutting, species richness increased slightly with the frequency of sward cuts from none, to one, to two cuts per year.

For phytophagous invertebrate species richness, three models made up the 95·0% confidence set, with all six fixed effects defining management and plant community composition being represented (Table 2). All six fixed effects were present in at least two of the three models. The phytophagous invertebrates showed a strong positive correlation with sward architecture, although the strength of this relationship was less pronounced than that seen with the predators, with a $c.$ 50·0% increase in species richness over the range of sward architecture measures found (Fig. 1a). Both forb and grass species richness were positively correlated with phytophagous invertebrate species richness, although this effect was less pronounced than that for sward architecture (Fig 2a,b). While the application of inorganic fertilizer resulted in a small increase in phytophagous invertebrate species richness, disturbance associated with both cutting and grazing resulted in a decrease (Fig. 3). In all cases, the overall effects of management were relatively weak, with no management practice resulting in a net change in species richness of greater than six species.
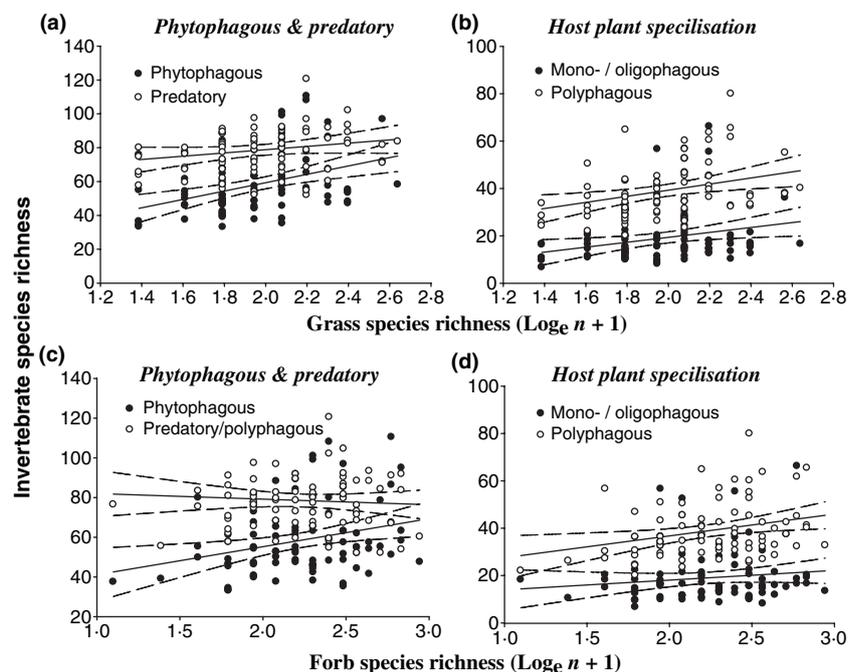
FEEDING GUILD AND INVERTEBRATE SPECIES RICHNESS

For the monophagous/oligophagous plant feeding invertebrates, three models explained the 95·0% confidence set, with all six management and plant community structure parameters being included in at least two models (Table 3). Again a strong positive correlation with sward architecture was the dominant effect, explaining increases in species richness of $c.$ 180% over the range of sward architecture values found within the field margins (Fig. 1c). Similarly, positive correlations were found with both grass and forb species richness (Fig. 2d,e), although the overall effects of these were less pronounced. Both grazing (Fig. 3) and inorganic fertilizer resulted in slight increases in

Table 2. The best set of general linear mixed models (95·0% confidence set) explaining the effects of management, plant composition and sward structure on the species richness of predatory and phytophagous invertebrates. AICc values, delta weight (Δ_i: the difference in AICc of the model in question and the best fitting model) and the model selection probability (w_i) are presented. The model selection probability has also been summed across all models where a predictor was present. Parameter estimates (β) were generated by averaging across all models, using the selection probabilities to weight this process. For the predictors grass species richness (Grass-SR), forb species richness (Forb-SR) and sward architecture (H_{Arch}), β_1 represents the averaged regression coefficient. For cattle grazing (Grazing) and inorganic fertilizer application (NPK) β_1 represents the difference in species richness relative to experimental plots not receiving these treatments. Also, β_1 and β_2, respectively, represent the difference relative to uncut field margins of plots cut once or twice in each year (Cutting). The prefix M refers to 'model', given in level order of greatest explanatory power

	Variable								
	Grazing	Cutting	NPK	Grass-SR	Forb-SR	H_{Arch}	AICc	Δ_i	w_i
Predatory									
M1	1	1	1	1	1	1	634·5	0·0	0·880
M1	1	1		1	1	1	640·1	5·6	0·054
M3	1	1	1		1	1	640·6	6·1	0·042
Summed selection probability	0·981	0·981	0·927	0·939	0·981	0·981			
β_1	−11·144	4·943	3·636	4·077	−6·01	22·645			
β_2		5·737							
Phytophagous									
M1	1	1	1	1	1	1	656·2	0·0	0·823
M2		1	1	1	1	1	661·2	5·0	0·068
M3	1	1		1	1	1	661·3	5·1	0·064
Summed selection probability	0·887	0·955	0·891	0·955	0·955	0·955			
β_1	−0·935	−1·226	2·189	7·012	10·009	31·381			
β_2		−5·713							
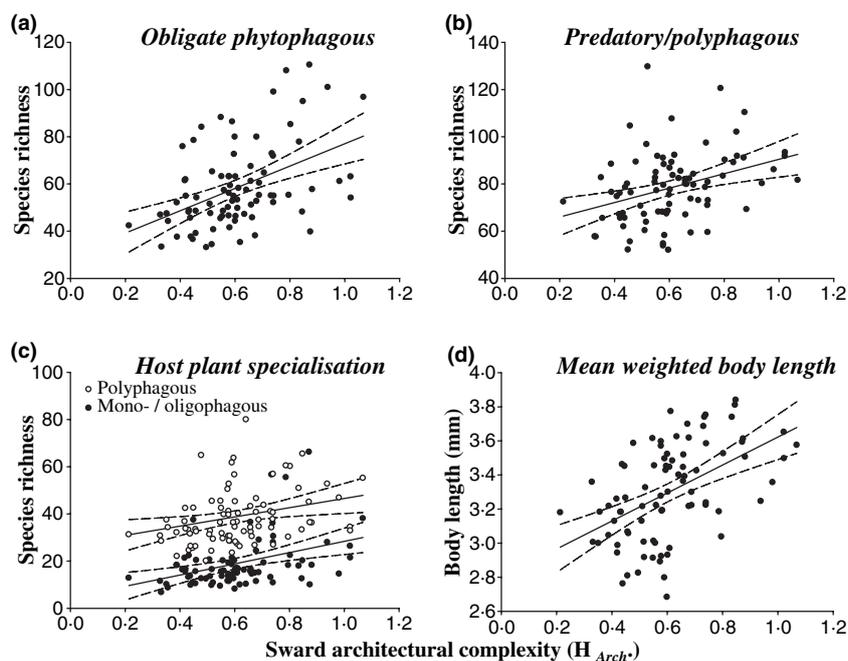
Fig. 1. Relationships between sward architectural complexity (H_{Arch}) and species richness of the (a) phytophagous, (b) predatory and (c) plant feeding invertebrates showing monophagous/oligophagous and polyphagous host plant specificity. Also shown is the relationship between sward architecture and the (d) weighted mean body length of invertebrates. Regression lines (solid line) and 95·0% confidence intervals (dashed line) are for univariate relationships only, and are included to provide a visual reference for the relationship.

Fig. 2. Change in invertebrate species richness in response to grass species richness for the (a) phytophagous and predatory trophic levels, and (b) plant feeding guilds showing monophagous/oligophagous or polyphagous host plant specificity. The same relationship is also shown for the response to forb species richness (c, d). Regression lines (solid line) and 95·0% confidence intervals (dashed line) are for univariate relationships only, and are included to provide a visual reference for the direction of the relationship.

monophagous/oligophagous species richness, although in both cases this increase was small (≤2 species). While the effect of a single sward cut per season differed little from no cutting management, two sward cuts did result in a decrease in species richness.

For the polyphagous plant feeders, only two models were included within the 95·0% confidence set, of which only the fixed effect of inorganic fertilizer, grass species richness, forb species richness and sward architecture were represented in one or more of these (Table 3). Again, sward architecture was the dominant effect causing a *c.* 60% increase in species richness

(Fig. 1c), although positive correlations were also found with both forb and grass species richness. For both forb and grass species richness the size of this correlation was larger than that seen for the monophagous/oligophagous feeding guild. In contrast to previous trends, the use of inorganic fertilizer resulted in a slight decrease in polyphagous invertebrate species richness.

WEIGHTED MEAN BODY LENGTH

The 95·0% confidence set for the weighted mean body length was represented by 14 models, within which only sward
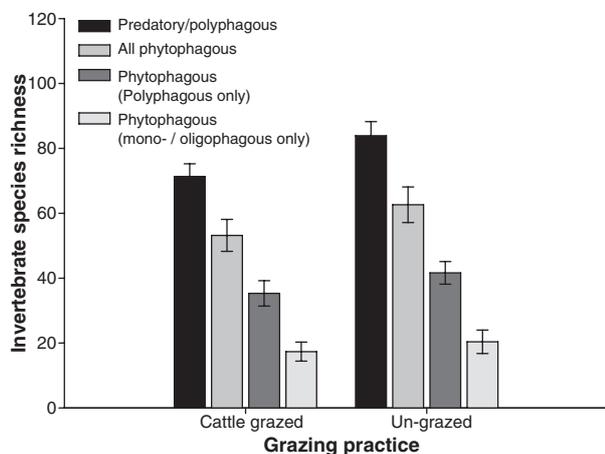
Fig. 3. Change in overall invertebrate species richness ($\pm$SE) according to trophic level and feeding guild in response to cattle grazing. The response shown represents the univariate relationship and is included to provide a visual reference of the relationship only.

architecture was consistently included as a fixed effect, while cutting was not represented at all (Table 4). In all cases, increases in mean body length were relatively small, not exceeding 1 mm over the range of any of the considered fixed effects. However, such a small increase in mean body length has a huge impact on biomass when the large numbers of invertebrates collected are considered. A 1 mm increase in weighted mean body length was, however, only seen for the positive correlation with sward architecture. In all other cases the extent of the change in mean body length was an order of magnitude lower. However, both forb and grass species richness were positively correlated with weighted mean body length, while grazing increased and inorganic fertilizer decreased body length.

Discussion

This study utilized a large-scale multi-site experiment to identify functional responses of invertebrates to the impacts of management extensification within agriculturally improved lowland grasslands. Using this experimental framework we identified sward architecture as a key driver of species richness across both invertebrate trophic levels and feeding guilds. It should be noted that this pattern of response to sward architecture is robust, even when the most speciose invertebrate taxa considered in this study (the beetles) were excluded from the analysis (Appendix S2). This confirmation of prediction (i) is in agreement with a well-established body of literature (e.g. Robinson 1981; Lawton 1983; Morris 2000; Woodcock *et al.* 2007a). The importance of architectural complexity for phytophagous taxa reflects patterns of resource utilization by invertebrates that may be split between different plant structures, such as roots, stems, leaves and flower or seed heads. In structurally complex swards, where the full range of these phenological structures develops, a single host plant may support many phytophagous species (Morris 2000). Similarly, architecturally complex swards provide an increased potential for niche differentiation for predatory taxa; for example, spider web structure and preferred location varies considerably between different species (Roberts 1987; Harwood, Sunderland & Symondson 2003). As sward architectural complexity increases, so does the availability of niches suitable for the construction of different web types, thereby promoting species coexistence (Robinson 1981). For ground-dwelling predators, refuges within the sward play a crucial role in habitat suitability, in particular tussock-forming grasses are crucial for many taxa, such as ground or rove beetles (Morris 2000).

Both phytophagous invertebrate species richness, as well as the species richness of the plant feeding guilds (monophagous/oligophagous and polyphagous) showed consistent positive correlations with forb and grass species richness. This is in

Table 3. The best set of general linear mixed models (95·0% confidence set) explaining the effects of management, plant composition and sward structure on the species richness of phytophagous invertebrates. For further details, see caption of Table 2

	Variable								
	Grazing	Cutting	NPK	Grass-SR	Forb-SR	H_{Arch}	AICc	Δ_i	w_i
Monophagous and oligophagous									
M1	1	1	1	1	1	1	593·6	0·0	0·906
M2	1	1		1	1	1	600·2	6·6	0·034
M3		1	1	1	1	1	600·3	6·7	0·032
Summed selection probability	0·94	0·972	0·938	0·972	0·972	0·972			
β_1	1·909	0·267	1·754	2·219	2·246	20·398			
β_2		−4·084							
Polyphagous									
M1			1		1	1	545·3	0·0	0·645
M2			1	1		1	546·5	1·2	0·354
Summed selection probability	0·000	0·000	0·999	0·354	0·645	0·999			
β_1	−0·001	0·001	−1·108	3·413	5·547	14·345			
β_2		0·001							

Table 4. The best set of general linear mixed models (95·0% confidence set) explaining the effects of management, plant composition and sward structure on the weighted mean body length of invertebrates according to host plant specificity. For further details, see caption of Table 2

	Variable								
	Grazing	Cutting	NPK	Grass-SR	Forb-SR	H_{Arch}	AICc	Δ_i	w_i
M1	1		1	1		1	7·2	0·0	0·146
M2	1		1		1	1	7·3	0·1	0·139
M3				1		1	8·1	0·9	0·093
M4			1			1	8·3	1·1	0·084
M5	1		1	1	1	1	8·4	1·2	0·080
M6			1	1		1	8·9	1·7	0·063
M7	1				1	1	9·0	1·8	0·060
M8		1			1	1	9·1	1·9	0·057
M9			1		1	1	9·2	2·0	0·054
M10	1		1			1	9·4	2·2	0·049
M11			1	1	1	1	9·9	2·7	0·038
M12						1	10·2	3·0	0·033
M13	1			1	1	1	10·4	3·2	0·030
M14	1					1	10·8	3·6	0·025
Summed selection probability	0·549	0·000	0·520	0·603	0·603	0·943			
β_1	0·063	0·001	−0·066	0·113	0·085	0·761			
β_2		0·003							

agreement with prediction (ii). While this relationship may be intuitively obvious (Haddad, Haarstad & Tilman 2000), it is not always the case that such a response is found (e.g. Koricheva *et al.* 2000). Indeed, where a restricted taxonomic group is investigated, inverse relationships have been found, particularly where many invertebrate species feed on a few host plants that are not necessarily found in floristically species-rich swards (Woodcock *et al.* 2007a). The rate of increase in polyphagous species richness in response to forb and grass species richness was higher than that seen for the monophagous/oligophagous plant feeders. This may reflect the fact that many of the plant species that became established in the higher diversity experimental plots tend to support large assemblages of polyphagous plant eating invertebrates, e.g. *Cirsium* spp. (Asteraceae).

For the phytophagous invertebrates, overall species richness was negatively affected by disturbance associated with grazing and cutting, although not that of inorganic fertilizer application. The overall size of these effects was, however, relatively small. As suggested in prediction (iii), the response of the monophagous/oligophagous feeding guild to disturbance was greater than that seen for polyphagous plant feeders. Indeed for the polyphagous feeding guild there was no response to cutting or grazing. This indicates that the wider resource base of the polyphagous invertebrates makes them less susceptible to disturbance than would be expected for species dependent on one or a few host plants. It does appear, however, that the intensity of disturbance is important. For example, cutting more than once a year has a negative impact on monophagous/oligophagous invertebrate species richness. It is likely that grazing and low frequency cutting promotes the establishment of key host plants within the sward by reducing competitive dominance of some of the grasses, such as *Lolium perenne* L. Where disturbance became more frequent (two sward cuts a

year) this appears to have had a negative impacted on some of the more disturbance-sensitive grassland plants. The exclusion of the speciose beetle taxa from the overall analysis resulted in the rejection of prediction (iii), at least in the case of disturbance caused by grazing (Appendix S2). The polyphagous invertebrates, rather than showing no response, now showed a reduction in species richness where grazing occurred, and one that was greater than that seen by the monophagous/oligophagous invertebrates. It is likely that this response reflects the negative effects that loss of foliage associated with grazing has on the planthoppers, a taxa with a large number of polyphagous species. It is also worth considering that with the removal of the beetles, few species remained that were monophagous/oligophagous, and as such an analysis without the inclusion of the beetles is probably of limited value.

The impact of inorganic fertilizer (NPK) on species richness was generally weak, both across trophic levels and within the phytophagous feeding guilds. Unexpectedly, it resulted in small increases in species richness for both the predatory and phytophagous trophic levels. For the predatory taxa, which showed the strongest response to NPK fertilizer, such an increase in species richness could be attributed to increased prey abundance within high nitrogen plots (Haddad *et al.* 2000). Typically, however, species richness for phytophagous taxa would be expected to be reduced in response to the application of fertilizer, as has been found elsewhere (Morris 1992; Haddad *et al.* 2000). The observed trend of increasing species richness in response to NPK fertilizer is not, though, without precedent (Callaham *et al.* 2003). Given the overall range of effects of NPK fertilizer on species richness found in this study its importance is arguably negligible. It is possible that the weak trends in response to NPK seen here may reflect high variability in the retention of NPK fertilizer on field margins, according to local water run-off conditions (Frame 2000).

Certainly a better understanding of the impacts of NPK fertilizer may have been provided by considering a continuous measure of its effect, such as vegetation nitrogen content.

Disturbance associated with management was not found to have a negative effect on weighted mean body size, rejecting prediction (iv). Indeed any effect of management on mean body size was so small as to be unimportant. Although the exclusion of the beetles form the analysis did result in grazing having a negative effect on invertebrate body size, the magnitude of these effects was again too small to be of importance (Appendix S2). However, as disturbance (particularly in the case of cutting and grazing) negatively impacts sward architecture (Morris 2000; Woodcock *et al.* 2007a), there may be some indirect support for the prediction as mean body length increased with sward architectural complexity. While the impact of sward architecture on body length was small, its ultimate impact on invertebrate biomass may have been much greater (Saint-Germain *et al.* 2007). For example, if mean body length is converted to mass, using established regression equations (Rogers, Hinds & Buschbom 1976), an increase in mean body length of 3·0–3·6 mm (within the predicted range) would increase invertebrate mass per unit area by *c.* 60% assuming constant density. As invertebrate abundance typically increases with sward architecture (Woodcock *et al.* 2007a), this estimate would be conservative. Therefore, architecturally complex swards will be characterized not only by higher rates of metabolic turn over (Saint-Germain *et al.* 2007) but also by the provision of more food resources for higher trophic levels, such as birds (Vickery *et al.* 2001).

In conclusion, there is a clear potential for modifying plant communities in improved grassland field margins to benefit both invertebrate species richness, as well as broader functional patterns defined by trophic structure and underlying body size. Promoting plant species richness, both grass and forb, and most significantly sward architectural complexity, seems to be crucial when manipulating plant communities to achieve management goal. How such modifications of plant community structure are achieved may not be as important as the effects that these management practices have on plant species richness or sward architecture. However, extensification of grazing and cutting regimes (i.e. reductions in their intensity and frequency) are likely to be crucial in increasing both sward architecture and plant species richness (Blackstock *et al.* 1999; Morris 2000). It is important to note that in contrast to arable agriculture, extensification of field margin areas will often necessitate their isolation from the remainder of the field by livestock exclusion fencing. The cost of this fencing will vary considerably, depending on whether it is temporary electric fencing or a permanent structure, and as such may set limitations on the financial viability and thus wide-scale implementation of management approaches used to manipulate sward structure. Indeed, it may well be the case that in some situations sacrificing a single field of equivalent areas to many field margins may represent a more financially viable option than fencing off large areas of field margins. Independent of this issue, our results indicate that the measures of plant community composition considered are key drivers of the underlying functional composition on the invertebrate community. This is of considerable importance as changes in both trophic level and guild structure suggest shifts in functional composition of the invertebrate community, in particular the underlying pattern of trophic links between species. Such changing patterns of trophic linkages will have implications for the provision of ecosystem services provided by the grasslands (e.g. pollinations, biocontrol or nutrient cycling), as well as the susceptibility of these habitats to environmental change (Thebault & Loreau 2006).

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Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. Summary of raw species richness values for the separate invertebrate taxa in response to treatment and year

Appendix S2. Summary tables for a repeated analysis using the information theoretic approach described in the methodology, where the beetles, the most speciose of the invertebrate taxa, have been excluded

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