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Science into practice - how can fundamental science contribute to better management of grasslands for invertebrates?

Running title: grassland invertebrate conservation

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Abstract

1. Grasslands are diverse and extensive but are declining in extent in some parts of the globe. Grassland invertebrates can be numerically abundant and are crucial to ecosystem functioning through their roles in herbivory, nutrient cycling and pollination. Most European grasslands are modified through agricultural practices. Indeed semi-natural grasslands, which often host the most diverse invertebrate assemblages, have suffered catastrophic losses over the last century.

2. Much research exists on grassland management, mainly from Europe, ranging from identifying optimum management of high-quality grasslands through to assessing measures to enhance low-quality grasslands, though most such projects focus solely on the plant assemblage. Monitoring that has been carried out on invertebrates indicates a varied response with invertebrate assemblages often being limited by such factors as lack of habitat connectivity, inappropriate cutting regime and the particular plant species used in enhancement projects.

3. There is a need to promote grassland management that recognises and addresses these key factors whilst also carrying out research into how best to combine the multiple ecosystem services and human benefits that are associated with grasslands.

Key words: agriculture, cutting, dispersal, fragmentation, grazing, habitat patch, insect, invertebrate, landscape, restoration

Introduction

Grasslands represent a diverse biotope that ranges from natural self-sustaining systems to those that are entirely artificially created. They cover approximately 40% of the world's land surface (excluding Greenland and Antarctica) (White *et al.*, 2000), and provide a wide range of goods and ecosystem services, but are primarily seen as highly significant as a resource for agricultural production (Balvanera *et al*., 2006; Jauker *et al*., 2009; van Eekeren *et al*., 2010). In some areas there have been significant declines in grassland extent. For example, the extent of all lowland grasslands (permanent pasture, rough grazings and leys) in England and Wales fell from 7.8M ha in the 1930s to 4.8M ha (a 38% decline) in the 1980s (Fuller, 1987) whilst in member states of the European Union, grassland extent declined by 12.8% from 1990 to 2003 (FAO, 2006). The decline has been especially acute for semi-natural grasslands. For example, only 3% of the area in existence in England and Wales in the 1930s survived to the 1980s (Fuller, 1987) and just 3.6% of Europe's grasslands lie within protected areas (White *et al.*, 2000). In the absence of wild large herbivores, most grassland areas have been maintained by farming and thus ecologists must work with land managers and policy makers to ensure the maintenance of biologically-rich and functioning grassland ecosystems (Pärtel *et al.*, 2005).

Terrestrial arthropods are integral to the full functioning of grassland ecosystems through numerous roles such as herbivory, nutrient cycling and pollination (e.g. Losey & Vaughn, 2006). Furthermore they form a diverse, though often neglected, component of grassland biodiversity. They are often numerically abundant with populations and assemblages that can respond rapidly to perturbation and can thus be especially useful as indicators in studies of grassland condition (e.g. Hollier *et al.*, 2005; Korosi *et al.*, in press). Recent thinking about managing natural resources has shifted away from a species-centred approach to one looking at the roles that component parts play in the functioning of whole ecosystems (e.g. Balmford & Bond, 2005). From an invertebrate ecology point of view, this approach has started to focus attention on such factors as functional roles played by invertebrates and the impacts of management and other perturbations on invertebrate assemblages (e.g. Biedermann *et al.*, 2005). Research on the role of invertebrates within ecosystem functioning and ecosystem services is, though, still in its infancy (Didham *et al.*, 2010; Seppelt *et al*., 2011).

As diverse as grasslands are, so is management aimed at maintaining them. There remain significant knowledge gaps in that much of the research into management does not explicitly consider the requirements of invertebrates. For example, high-quality natural or semi-natural grasslands, typically in Europe those that have not been subject to nutrient input, have seen considerable research into appropriate vegetation management. Calcareous grasslands are now widely recognised for their biodiversity value, as they host some of Europe's most species-rich plant and insect assemblages (van Swaay, 2002; WallisDeVries *et al.*, 2002).

Much of the remaining area of this grassland type is under conservation management and the restoration of former chalk grassland now represents a key mechanism for increasing their area. Such management usually focuses on the plant assemblages but success in terms of the reassembly of invertebrates has been limited (Mortimer *et al.*, 2002; Woodcock *et al.*, 2010a).

Of course most European grasslands are modified, primarily by agricultural practices (e.g. Stoate *et al*., 2009). Even modified grasslands, though, have the potential to support important assemblages or populations of rarer species (e.g. Alexander, 2003; Littlewood & Stewart, 2011) as well as assemblages that can be important food resources for higher trophic levels such as birds (Vickery *et al*., 2001). A greater understanding of how such assemblages relate to grassland structural characteristics would be beneficial in terms of maintaining and enhancing population sizes of many species, (e.g. Helden *et al.*, 2010; Trivellone *et al*., in press). In recent years, land management policy has reflected increased interest in reversing the impacts of agricultural intensification. This may range from reversing biodiversity loss in less intensively managed grasslands by preventing over-grazing (Redpath *et al.*, 2010), to encouraging appropriate incentives for preventing the abandonment of traditional management (Stoate *et al*., 2009). Furthermore, there has been interest in landscape conservation and restoration to maintain habitat heterogeneity and connectivity in the light of research showing that patch isolation can be detrimental not just to the range of species occurring, but also to ecosystem services such as pollination success (Goverde *et al.*, 2002) and natural pest control (Steffan-Dewenter & Tscharntke, 2002).

This short review and the Special Issue that it introduces aims to explore and develop the key themes identified above. The papers that follow stem from a symposium on grassland insect conservation held as part of the European Congress of Conservation Biology in Prague in 2009 together with other highly relevant contributions. These papers aim to raise the profile of grassland invertebrates within conservation science by showing the sensitivity of invertebrates to perturbation, their importance for demonstrating grassland condition and functioning, and how knowledge of their fundamental ecology can contribute to the practical management of various grassland types.

Management of existing grasslands

Typically, the primary aim of invertebrate conservation within existing grasslands is to maintain species richness while retaining any rare or local species, although these aims may sometimes conflict with each another. Invertebrate diversity is often, but not invariably, strongly correlated with plant diversity (Schaffers *et al*., 2008). Partly this may be simply due to plant and invertebrate species each responding to the same extrinsic driver such as temperature or wetness. For phytophagous species in particular, though, dependence on specific host plants may result in a strong link between plant and invertebrate assemblages (Woodcock *et al*., 2010b).On the other hand, though, the architectural structure of the sward is important for both zoophagous and phytophagous species, such that short swards generally contain a lower abundance and reduced diversity of insects compared to taller ones (Dennis *et al*., 1998; Morris, 2000). This relationship is underpinned by both the greater biomass of structurally complex swards as well as the greater range of niches available for invertebrates. Certain invertebrate groups are known to be strongly vertically stratified (e.g. Auchenorrhyncha; Andrzejewska, 1965; Brown *et al*., 1992) or dependent upon the physical architecture of the vegetation (e.g. Araneae; Gibson *et al*., 1992), whilst removal of tall flowering structures in particular, reduces the diversity of pollinators, seed feeders, gallers and other insects that exploit flowers and associated stems (Volkl *et al*., 1993; Woodcock *et al*., 2009). The relationship between sward structure and invertebrate populations may, though, be less straightforward as sward height may be a proxy for a further driver. For example, in this issue, Dittrich & Helden (in press) show how populations of phytophagous and predatory invertebrates can be enhanced in taller sward islets where the driver (for the phytophagous species at least) appears to be a higher nutrient content of the taller vegetation.

Conservation management of grasslands typically aims to arrest the natural succession to scrub and woodland by grazing, cutting or, more rarely, burning; the objective being to check the spread of fast-growing competitive plant species and to maintain low system fertility by removing biomass (e.g. Swengel, 2001; Watkinson & Ormerod, 2001). Much research has been focused on how these management operations can be fine-tuned to promote diversity by varying their intensity, frequency, duration, seasonality and in the case of grazing, by using different species or breeds of domesticated herbivore (Watkinson & Ormerod, 2001). All of these have subtly different effects on the species composition and structure of the vegetation, and thereby on the associated invertebrates, although the details vary between functional and taxonomic groups (e.g. Morris, 2000). In general, low-intensity grazing is preferable to cutting because it is gradual rather than sudden, thus allowing insects to escape (Humbert *et al*., 2009), grazers tend to feed on the fast-growing more palatable plants which may need to be suppressed, and their trampling and local fertilization through deposition of dung and urine promotes heterogeneity in the sward (Dennis *et al*., 1998; Helden *et al*., 2010). Grazing and browsing by wild vertebrate herbivores, such as rabbits, can have additional or separate effects to domestic herbivores which may further influence the constituent invertebrate assemblage (Fisher Barham & Stewart, 2005).

The greater abundance and diversity of invertebrates in taller grasslands often brings invertebrate conservation into conflict with the objective of preserving plant diversity (e.g. Kruess & Tscharntke, 2002). In some cases, the use of heavier grazing animals to promote micro-topographic heterogeneity, and patches of bare ground for invertebrates, is incompatible with the requirements of delicate plant species such as orchids (e.g. Tamis *et al*., 2009; Hutchings, 2010). Inevitably with so many species involved, each with their own particular micro-habitat requirements, any one management prescription will favour certain invertebrate taxonomic groups over others (e.g. Morris, 1978). Even within relatively narrowly-defined groupings, there will be wide differences in responses to management. For example, grassland butterflies range widely in mean sward height preference from <2 to >30 cm (NCC, 1986). Faced with the challenge of maintaining a large number of species with widely differing habitat requirements, often within a relatively small area, one solution is to impose small-scale rotational management to generate a mosaic of different grassland heights, ages and successional stages, thus producing maximal heterogeneity at a variety of scales (Pöyry *et al*., 2004).

Re-creation of grasslands

There is general agreement that the *de novo* re-creation of grasslands that resemble species-rich assemblages that are highly prized by conservationists will take a very long time indeed, perhaps hundreds of years (Hutchings & Stewart, 2002). Simple abandonment of arable land is unlikely to set natural succession on a trajectory to species-rich grassland because of the high nutrient residues, especially of phosphorus, and the absence of appropriate plant propagules (Bakker & Berendse, 1999; Pywell *et al*., 2002). Attempts to manage the path of plant succession have shown that only very heavy grazing will achieve a community that starts to resemble ancient species-rich grassland (Gibson & Brown, 1992), a result that is reflected by certain invertebrate groups (Gibson *et al*., 1992). A major limitation to the success of such re-creation attempts is dispersal of the target species into the area, rare species in particular tending to be poor dispersers (Batary *et al*., 2007; Knop *et al*., 2011). In the case of plants, attempts have been made to overcome this by sowing seed mixtures, strewing hay or inserting plant plugs to establish an appropriate assemblage of species (e.g. Bakker & Berendse, 1999; Pywell *et al*., 2002). Indeed, as demonstrated by Woodcock *et al*. (in press) in this issue through an example where ex-arable land was being managed to recreate species-rich lowland hay meadow, the introduction of target plants can prove crucial to facilitating reassembly of phytophagous beetle species. While such management practices are potentially economical to undertake for plants, though, dispersal limitation may restrict resultant invertebrate populations and overcoming this is likely to be both hard and costly to implement. In the majority of cases colonisation will be by natural immigration only and thus it is likely that targeting restoration sites within landscapes with existing large areas of species rich grassland will help colonising invertebrates overcome dispersal limitation (Woodcock *et al*., 2010a). As the order in which species arrive during restoration (so called priority effects) may have important long-term implications for community structure, long-term restoration success may be strongly affected by the availability of source populations of colonising invertebrates (Young *et al*., 2005).

For the most part, and particularly in the case of phytophagous invertebrates, the establishment of species in such experiments is often determined by the restoration success of plants. This is seen, for example, in Hemiptera (Morris, 1990), Coleoptera (Mortimer *et al*., 2002), and Lepidoptera (Maccherini *et al*., 2009) although often the invertebrate communities of restored grasslands represent only a component of the target species-rich grassland communities.

Enhancement of low quality grasslands

While the biodiversity benefits of grassland restoration may be potentially large, as a conservation measure it is typically costly, complicated and time consuming to implement (Bakker & Berendse, 1999; Willems, 2001; Walker *et al*., 2004). The associated expense means that uptake may be restricted to sites that meet specific minimum habitat requirements, as occurs in the case of grassland restoration sites within the UK agri-environmental schemes that are geared towards more biodiverse sites (Natural England, 2008). For this reason large areas of grassland that are unsuitable for restoration remain floristically species poor and structurally homogenous, and as such are of low biodiversity value for invertebrates (Morris, 2000; Potts *et al*., 2009; Woodcock *et al*., 2009).

The diversification of low-quality grassland can be difficult because few germination sites exist in a closed sward, limiting the capacity of new species to invade, and seedlings suffer intense competition from pre-established plants (Edwards *et al*., 2007). Intense grazing or scarification of the sward may help to break up the vegetation to enable new species to colonise, a technique that would also favour certain invertebrate groups (Woodcock *et al*., 2008). Such grasslands may, though, be suitable for more modest enhancement management, which aims to increase the levels of biodiversity associated with existing habitats of low conservation value, without attempting to replicate a specific community as would occur in restoration as described above. In Europe, such enhancement is often implemented as a result of agri-environment schemes which aim to compensate farmers for modest changes to their management practices (Young *et al*., 2005). Following in this issue are two such examples of how invertebrate populations can be enhanced in agriculturally productive landscapes. Firstly Cole *et al*. (in press) demonstrate how fencing off waterways in intensively-managed grasslands to exclude livestock can promote habitat heterogeneity and hence invertebrate populations, even in relatively narrow buffer strips. Secondly Trivellone *et al*. (in press) provide evidence that low-intensity management, in particular infrequent cutting and low pesticide use, can promote invertebrate biodiversity of grasslands and associated habitats within vineyards.

Management associated with grassland enhancement is often straightforward and the intended goals of such practices may be diverse, although they are rarely, if ever, centred on invertebrates. In addition, such management is not normally intended to benefit rare or threatened species directly, although by creating stepping stones and corridors across the landscape it can promote population persistence in higher quality grassland habitats (Van Geert *et al*., 2010). In England, for example, five grassland enhancement options exist for lowland grasslands under the entry-level agri-environmental scheme, each representing simple management changes to existing improved grassland management, such as reduced fertiliser input (< 50 kg/ha/year N) or mixed stocking of cattle and sheep (DEFRA, 2005).

It is questionable whether the benefits accrued for invertebrates as a result of these management options will result in large scale biodiversity gains (Pywell *et al*., 2010). In many cases the aims of these schemes focus on increasing the overall biomass of invertebrates to provide food resources for higher trophic levels, such as farmland birds (Vickery *et al*., 2001; DEFRA, 2005). This is often achieved by introducing variation in the architectural structure of the sward and can be done by two means. Firstly, heterogeneous grazing management promotes the development of tussock grasses that are vital for many invertebrates (Bayram & Luff, 1993; Dennis *et al*., 1998; Morris, 2000). Secondly, temporal variation across landscape management can contribute to the maintenance of invertebrate diversity. For example, varying the timing of grass cutting can reduce the impacts on invertebrates of what might otherwise be a catastrophic loss of sward structure (Morris, 2000; Humbert *et al*., 2009).

In some grasslands, maintenance of, or simple changes to, existing management, such as in cutting, grazing and fertiliser regimes, can have a large positive effect on the biodiversity value of these habitats (Dennis *et al*., 1997; Dennis *et al*., 2004. In this issue, for example, Littlewood *et al*. (in press) describe grazing impacts on Auchenorrhyncha assemblages in upland rough grassland and show that maintaining a grazing intensity mosaic, including ungrazed areas can substantially enhance abundance and diversity. Likewise for Hemiptera as a whole, Korosi *et al*. (in press) demonstrate that vegetation height is the primary driver of assemblages and that variations in sward height produced by different cattle-grazing regimes helps to maintain diverse assemblages. Low-key grassland management changes may have only limited success in increasing floristic diversity in agriculturally improved grasslands, particularly where there is a high level of residual fertility, resulting in competition for space within the sward (Woodcock *et al*., 2007; Potts *et al*., 2009; Woodcock *et al*., 2009). Under these circumstances the establishment of forbs within the sward normally requires some form of direct introduction of target species. As plants differ considerably in the numbers of invertebrate species associated with them, there is considerable scope for enhancing existing grasslands by sowing a few well-selected species. In particular, the introduction of commercially available plants that are both known to support a high diversity of phytophagous invertebrates as well as being competitive enough to be able to persist in improved grass swards has the potential to provide dramatic benefits for invertebrates (Koricheva *et al*., 2000; Mortimer *et al*., 2006; Potts *et al*., 2009; Pywell *et al*., 2010). This can be achieved at comparatively low cost relative to restoration management and may be suitable for the enhancement of existing floristically species poor swards (Mortimer *et al*., 2006; Pywell *et al*., 2010; Woodcock *et al*., in press). To this end, one technique that has shown great promise is the introduction of hemiparasitic plants to check the growth of the more vigorous plant species, facilitate the establishment and survival of introduced forbs and thereby promote greater diversity. For example, *Rhinanthus minor* is hemiparasitic on grasses and is now widely proposed as a tool for the diversification of grasslands (Pywell *et al*., 2004). Recent evidence indicates a positive effect on abundance and diversity of invertebrate herbivores and predators, indicating a community-wide response (Hartley, John, Massey, Stewart & Press, unpublished data).

Influence of the landscape matrix

Management of grassland and its impact on insect populations is usually approached at a site scale with the role of the surrounding matrix until recently only rarely considered. For conservation of especially rare species it may be necessary to carry out habitat management at a very specific site or colony (e.g. Young & Barbour, 2004) though isolated insect populations in habitat that remains apparently suitable may be at increased risk of extinction (e.g. Tscharntke *et al*., 2002; Goulson *et al*., 2008). The role of the surrounding landscape in regulating or structuring insect assemblages is, however, being gradually recognised and indeed, at the assemblage level, may explain more of the variation between sites than do finer scale habitat characteristics (e.g. Marini *et al*., in press).

This issue shows in particular how the landscape matrix interacts with species mobility in determining species distributions and assemblage make-up. For example Pokluda *et al*. (in press) provide an example of landscape-scale variation in habitat usage by a rare ground beetle with, in this case, forest habitats potentially providing a complete barrier to movement. Developing this theme, Wamser *et al*. (in press) demonstrate that trait-specific effects, such as dispersal-ability, determine how the landscape influences different elements of carabid biodiversity and thus demonstrate that habitat corridors may assist movement of species which are less able to disperse across barrier to habitat patches. Likewise Marini *et al*. (in press) shows that species mobility strongly influences species- turnover between Orthopteran populations and that assemblages may be enhanced by increased connectivity of meadows at the landscape scale.

Features of the landscape matrix may affect grassland insects in a number of ways. Physical landscape influences on invertebrates may be linked to protection from the elements, such as the preference shown by some butterflies for meadows benefiting from the sheltering effect of adjacent woodland (e.g. Marini *et al.*, 2009), or may be more directly related to movement within the landscape (e.g. Jauker *et al*. 2009). Resource-related influences may be linked to the need for connectivity of habitat patches in situations in which food availability is unpredictable (Johst *et al.*, 2006). Many species, especially those with specialised habitat requirements, exist to a greater or lesser extent in a metapopulation structure with smaller or marginal sites requiring occasional recolonisation from source colonies and with a higher proportion of unoccupied patches in a more fragmented landscape (e.g. Batary *et al*., 2007; Brückmann *et al.*, 2010).

The way in which aspects of the landscape matrix impact on invertebrate populations varies between different species or assemblages. For numerous groups, e.g. Auchenorrhyncha (Littlewood *et al.*, 2009) and Lepidoptera (Ries & Debinski, 2001), generalist species have been shown to disperse further than specialist species and so they are likely to respond to the landscape on a larger scale (Batary *et al*., 2007; Oliver *et al.*, 2010). This can have implications for stability of populations. Thus, a heterogeneous landscape, in which a range of resources and microclimates can help buffer against perturbation, may promote greater stability in populations of generalist species than specialists (Oliver *et al.*, 2010). There are other patterns that are consistent across more than one insect group. For example, the size and relative isolation of grassland habitat patches may be more significant limiting factors for predatory insects. This was shown by Stoner & Joern (2004) who demonstrated that Coccinellidae find it difficult to re-colonise after local extinction, while Zabel & Tscharntke (1998) showed that a range of predatory Heteroptera and Coleoptera were more affected by habitat isolation than were herbivores. Indeed patch connectivity in complex landscapes is recommended as a means of ensuring maximum efficiency of predator populations for pest-control purposes in agricultural grasslands (Tscharntke *et al.*, 2007).

Given the influence of the landscape matrix it may be presumed that grassland restoration and enhancement would have the greatest impact on insect populations at sites where it increases connectivity with other patches (Woodcock *et al*., 2010b; Knop *et al*., 2011). Defining optimum minimum distances and identifying patches between which individuals have moved is, though, very difficult. Movement of individual insects along habitat corridors or recolonisation of experimentally created habitat patches can be monitored on a small scale (e.g. Söderström & Hedblom, 2007; Littlewood *et al.*, 2009), whilst gene-flow can be assessed between isolated populations over greater distances (e.g. Darvill *et al.*, 2006).In such cases, though, findings are likely to be so species and site-specific as to preclude any useful general recommendations. Instead more general messages, perhaps based on re-instating ecosystem services, must be sought and promoted.

Concluding remarks

The biodiversity of grassland invertebrates helps to maintain numerous ecosystem services (Sutcliffe *et al*., 2003; Woodcock *et al*., 2010b; Knop *et al*., 2011), plays a crucial role in the structure of competitive interactions between plants (Rand, 2003), can underpin grassland restoration (De Deyn *et al*., 2003) and provides food for higher trophic levels (Vickery *et al*., 2001). In addition, the conservation of at least some invertebrates carries high societal value, although this is often limited to charismatic species such as the butterflies (Fleishman & Murphy, 2009). How we manage this biodiversity typically falls somewhere along a spectrum, ranging from relatively cheap (per unit area) low level changes in management applied at large spatial scales (Jeanneret *et al*., 2003; Schweiger *et al*., 2005; Woodcock *et al*., 2009), to expensive and targeted management regimes that benefit a few species at a particular site (Thomas, 1991). Changing patterns of land use, climatic variation and the need to provide food security means that the pressures on grassland biodiversity are only likely to increase over the coming decades (Stoate, 2009). For this reason, it is likely to become increasingly important to incorporate invertebrate biodiversity into the more general concept of multifunctional grasslands (Kemp & Michalk, 2007). Under such a premise, the conservation of grasslands as a whole, including that of invertebrates, will have to be presented to society within a wider package of benefits that include food production and quality, climate change amelioration, revitalising crop lands, protecting water quality and cultural heritage value (Kemp & Michalk, 2007; Stoate *et al*., 2009). If a long-term goal of maintaining invertebrate biodiversity in grasslands is to be achieved, then future research will need increasingly to consider how management will benefit not just the immediate conservation goals of a particular taxon, but also these wider objectives that are important to society as a whole.

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