Rothamsted Repository Download

A - Papers appearing in refereed journals

Brooks, D. R., Storkey, J., Clark, S. J., Firbank, L. G., Petit, S. and Woiwod, I. P. 2012. Trophic links between functional groups of arable plants and beetles are stable at national scale. *Journal of Animal Ecology.* 81 (1), pp. 4-13.

The publisher's version can be accessed at:

- https://dx.doi.org/10.1111/j.1365-2656.2011.01897.x

The output can be accessed at: https://repository.rothamsted.ac.uk/item/8q9wx.

27/03/2019 11:38   repository.rothamsted.ac.uk   library@rothamsted.ac.uk

Trophic links between functional groups of arable plants and beetles are stable at a national scale

David R. Brooks[1],*, Jonathan Storkey[1], Suzanne J. Clark[2], Les G. Firbank[3], Sandrine Petit[4] and Ian P. Woiwod[1]

[1]*Department of Plant and Invertebrate Ecology, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK;*
[2]*Department of Biomathematics and Bioinformatics, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK;*
[3]*Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT; UK; and* [4]*INRA, UMR 1210 Biologie et Gestion des Adventices, F-21000 Dijon Cedex, France*

Summary

1. There is an urgent need to accurately model how environmental change affects the wide-scale functioning of ecosystems, but advances are hindered by a lack of knowledge of how trophic levels are linked across space. It is unclear which theoretical approach to take to improve modelling of such interactions, but evidence is gathering that linking species responses to their functional traits can increase understanding of ecosystem dynamics. Currently, there are no quantitative studies testing how this approach might improve models of multiple, trophically interacting species, at wide spatial scales.

2. Arable weeds play a foundational role in linking food webs, providing resources for many taxa, including carabid beetles that feed on their seeds and weed-associated invertebrate prey. Here, we model associations between weeds and carabids across farmland in Great Britain (GB), to test the hypothesis that wide-scale trophic links between these groups are structured by their species functional traits.

3. A network of *c.* 250 arable fields, covering four crops and most lowland areas of GB, was sampled for weed, carabid and invertebrate taxa over 3 years. Data sets of these groups were closely matched in time and space, and each contained numerous species with a range of eco-physiological traits. The consistency of trophic linkages between multiple taxa sharing functional traits was tested within multivariate and log-linear models.

4. Robust links were established between the functional traits of taxa and their trophic interactions. Autumn-germinating, small-seeded weeds were associated with smaller, spring-breeding carabids, more specialised in seed feeding, whereas spring-germinating, large-seeded weeds were associated with a range of larger, autumn-breeding omnivorous carabids. These relationships were strong and dynamic, being independent of changes in invertebrate food resources and consistent across sample dates, crops and regions of GB.

5. We conclude that, in at least one system of interacting taxa, functional traits can be used to predict consistent, wide-scale trophic links. This conceptual approach is useful for assessing how perturbations affecting lower trophic levels are ramified throughout ecosystems and could be used to assess how environmental change affects a wider range of secondary consumers.

Key-words: agro-ecosystem, biodiversity, community dynamics, Farm Scale Evaluations, granivory, plant–insect interactions

Introduction

Global biodiversity declines are being driven by rapid, anthropogenically mediated change (Chapin *et al.* 2000).

Although there has been a bias towards considering biodiversity trends alone, models describing effects on ecosystem function are now regarded as indispensable precursors to understanding and managing the consequences of such change (Purvis & Hector 2000; Kremen 2005). However, the development of such models presents considerable challenges (Lavorel *et al.* 1997). For example, modelling of ecosystem

*Correspondence author: E-mail address: david.brooks@rothamsted. ac.uk

dynamics is critically impeded by a lack of knowledge of how trophic levels are linked in ecosystems (Tylianakis *et al.* 2008). A number of theoretical approaches to modelling such interactions have emerged, ranging from mechanistic modelling of pairwise species interactions (May 1974) and consumer resource models (Holt, Grover & Tilman 1994) through to complex assessments of food webs (McCann 2007). Opinion is, however, divided about which approach is best, or indeed whether any of them can contain the complexity of interactions in multi-species systems (Simberloff 2004). One way of improving this theoretical framework, that is, increasingly gaining favour, is the incorporation of taxa functional traits into models (De Bello *et al.* 2010). For example, carabids can have trait-mediated responses to landscape composition (Vandewalle *et al.* 2010), land disturbance and stress induced by habitat changes (Ribera *et al.* 2001), and flooding intensity (Lambeets *et al.* 2008). This approach provides a tractable route to modelling complex interactions because species traits are usually linked to the functions that they perform within ecosystems. Furthermore, these functions often vary in their importance, both for the viability of an ecosystem or the services that it delivers (Zavaleta & Hulvey 2004).

Lavorel & Garnier (2002) described the hypothesis that plant functional traits will determine the response of plant communities to the environment and, in turn, affect ecosystem processes. This concept can be extended to analyse the effect of plant traits on the responses of other functionally related taxa, predisposed to such links by their own traits. Evidence is growing that this hypothesis is a powerful tool (Kremen 2005), because when there is concordance between these 'effect' and 'response' traits modelling their relationship is a tractable way of understanding profound changes in ecosystem function (Larsen, Williams & Kremen 2005; Petchey & Gaston 2006; Schmitz 2008). This hypothesis has not, however, been extended to investigations of trophic linkages at large spatial scales. This is necessary to test the wider validity of this approach (Kremen *et al.* 2007), not least because quantifying geographical variation in ecological functioning is crucial to understanding how environmental change will alter biodiversity (Symstad *et al.* 2003).

The Farm Scale Evaluations (FSE) tested the effect of managing genetically modified crops on numerous groups of plants and invertebrates across most arable areas of Great Britain (GB). This study represents the largest field ecology experiment to date, providing paired data sets of arable plants and invertebrates, under contrasting crop management regimes, at an unprecedented spatial scale (Perry *et al.* 2003). These data therefore offer a unique opportunity to test different theoretical approaches to modelling links between trophic levels, thereby assessing the scope and universality of their application. In particular, the FSE generated data from conventionally managed half-field plots linking 236 species of arable weeds with 123 species of carabid beetles, covering 521 618 and 618 384 individuals of these groups, respectively. These plots accurately reflected the distribution and commercial production of four arable crops (Perry *et al.* 2003). These data provide an ideal model system for testing the coherence

of a trait-based approach for investigating how trophic levels interact. For example, responses of weeds to agricultural perturbations are strongly linked to their functional traits (Storkey, Moss & Cussans 2010). Similarly, carabids have trait-mediated responses to successional stages of plant communities in undisturbed habitats (Gobbi *et al.* 2010) and have facultative responses to feeding on weeds, including a preference for granivory in some species (Slansky & Panizzi 1986). For simplicity, throughout this paper, we describe any non-crop plants occurring in cultivated fields as weeds, but it should be noted that although all these species are important components of agro-ecosystem biodiversity, only a few are likely to cause significant reductions to crop yields.

Here, we use the FSE data to test the hypothesis described by Lavorel & Garnier (2002) within the context of two interacting trophic levels. To do this, we test the ability of arable weeds to respond to agricultural perturbations according to their traits and, in turn, affect a higher trophic level via links between these traits and the traits of carabid beetles. Within this system, the weed traits act as both 'response' and 'effect' traits, as defined by the hypothesis, by 'responding' to changes in the environment and then 'effecting' carabids. Similarly, the carabid traits act as the 'response' traits of a functionally related group, in our case by mediating their trophic responses to changing weed assemblages. We do this by grouping the numerous weed and carabid species available by their functional traits to test the following predictions: (i) weed taxa grouped by their traits will have similar functional responses across crops and regions of GB; (ii) carabid traits can be used to link patterns of their community variation to such wide-scale weed responses; (iii) groups of carabids expected, a priori, to have little response to weeds, owing to carnivorous feeding traits, will not have such links and (iv) groups of omnivorous carabids will have robust functional links with weeds, regardless of fluctuations in their invertebrate prey.

Materials and methods

EXPERIMENTAL DESIGN

Data were derived from the FSE project, which surveyed three spring crops between 2000 and 2002 and one winter crop between 2000 and 2003. Here, we provide a synoptic overview of the experiment; see Perry *et al.* (2003) and Firbank *et al.* (2003) for detailed descriptions of its design and methodology, respectively. The experiment used blocks of whole fields, with treatments allocated to half-field plots. Here, we use data from 249 conventionally managed half-field plots, which had an average size of 5·37 ha (SE = 0·193) and comprised of 65 beet, 58 maize, 67 spring oilseed rape and 59 winter oilseed rape plots. Half-field totals were used to model the wide-scale responses of taxa because variation was much higher between plots than within plots.

WEED EXPLANATORY VARIABLES

All weed species were counted in a 0·25 m × 0·50 m quadrat at points 2, 4, 8, 16 and 32 m from field edges, along 12 transects in

Table 1. Functional groups of weed taxa included in multivariate analyses. The summed abundance across each group is shown for the listed species, together with their percentage coverage of the wider count of all taxa in the respective group. Within groups, taxa are listed by rank abundance. Their total counts fall within the ranges: A = 35 001–*c*.111 500; B = 3001–35 000; C = 1001–3000; D = 501–1000 and E ≤ 501, with letters indicating emerged weed abundance given first and seed rain second

Functional group/species	Abundance		Ecological traits		
	Total	%	Germination	Seed mass: mean (range) in mm	First flowering
Group W1					
Galium aparine (C/D), *Fumaria officinalis* (D/–), *Anisantha sterilis* (E/D), *Avena fatua* (E/D), *Galeopsis tetrahit* (E/–)	4932	93·3	Autumn	7·26 (8·11–12·00)	May–June
Group W2					
Sonchus asper (B/A) *(S. asp)*, *Tripleurospermum inodorum* (C/B) *(T. ino)*, *Papaver rhoeas* (E/B), *S. oleraceus* (E/C), *S. arvensis* (E/D)	101 437	98·6	Autumn	0·34 (0·20–0·49)	April–June
Alopecurus myosuroides (B/B)				1·99	
Group W3					
Capsella bursa-pastoris (B/A) *(C. b-p)*, *Poa annua* (A/A) *(P. ann)*, *Stellaria media* (B/A) *(S. med)*, *Senecio vulgaris* (C/B) *(S. vul)*, *Veronica persica* (B/C) *(V. per)*, *Lamium purpureum* (C/D) *(L. pur)*	260 742	99·7	Autumn	0·45 (0·10–0·96)	March–April
Group W4					
Matricaria discoidea (C/B) *(M. dis)*, *Viola arvensis* (B/B) *(V. arv)*, *Solanum nigrum* (C/E), *Myosotis arvensis* (D/C) *(M. arv)*, *Urtica urens* (D/D) *(U. ure)*, *M. recutita* (E/E), *Spergula arvensis* (E/E)	64 239	97·6	Autumn	0·38 (0·04–0·70)	April–June
Geranium dissectum (C/B), *Aethusa cynapium* (C/C), *G. molle* (C/–)				1·65 (1·09–2·28)	
Group W5					
Chenopodium album (B/B) *(C. alb)*, *Sisymbrium officinale* (E/B) *(S. off)*,	70 912	98·9	Spring	0·45 (0·29–0·60)	May–July
Polygonum aviculare (B/B) *(P. avi)*, *Persicaria maculosa* (C/B) *(P. mac)*, *P. lapathifolia* (C/B) *(P. lap)*, *Sinapis arvensis* (C/C) *(S. arv)*, *Atriplex patula* (C/D) *(A. pat)*, *Fallopia convolvulus* (C/C) *(F. con)*				2·54 (1·30–6·70)	
Group W6					
Anagallis arvensis (C/E)	1547	85·2	Spring	0·50	June–July
Euphorbia helioscopia (E/E)				2·31	
Group W7					
Cerastium fontanum (E/C), *P. trivialis* (C/–), *Holcus lanatus* (–/C), *H. mollis* (–/C), *Trifolium repens* (E/E), *U. dioica* (E/E), *Taraxacum officinale* agg. (E/E), *Equisetum arvense* (E/–), *G. pusillum* (E/E), *Dactylis glomerata* (E/–)	17 809	75·6	Perennial	0·44 (0·10–0·90)	June–July
Elytrigia repens (C/E), *Cirsium arvense* (D/D), *Ranunculus repens* (D/–), *Rumex crispus* (–/D), *C. vulgare* (E/D), *Lolium perenne* (D/–), *R. obtusifolius* (E/E)				1·96 (1·30–2·90)	

each half-field, during surveys conducted in April–May, June–July and August for spring crops, and February–March, April–May and June–July for winter oilseed rape; see Firbank *et al.* 2003; for schematics of the sampling positions. Similarly, seed rain was sampled continuously from first anthesis, using eight mesh traps of 0·1 m diameter, sunk into the ground and divided between locations at 2 m and 32 m on four transects. Common UK weeds have been screened for a range of eco-physiological traits and seven emergent functional groups identified on the basis of life-history traits, seed mass and maximum height (Storkey 2006). These

groups and weed diversity measures were used to form explanatory variables for carabid responses (Tables 1 and S1, Supporting information). For emerged weeds and seed rain, partial principal component analyses (pPCA) were also conducted to assess community variation, using the CANOCO V4.5 program (Ter Braak & Šmilauer 2002). Smaller-seeded, autumn-germinating species (Group W3 and most species with these traits in Groups W2/W4) were separated from larger-seeded, obligate spring-germinating species (Group W5) (Figs 1 and S1, Supporting information). The sample scores on the first two pPCA axes were used to form additional
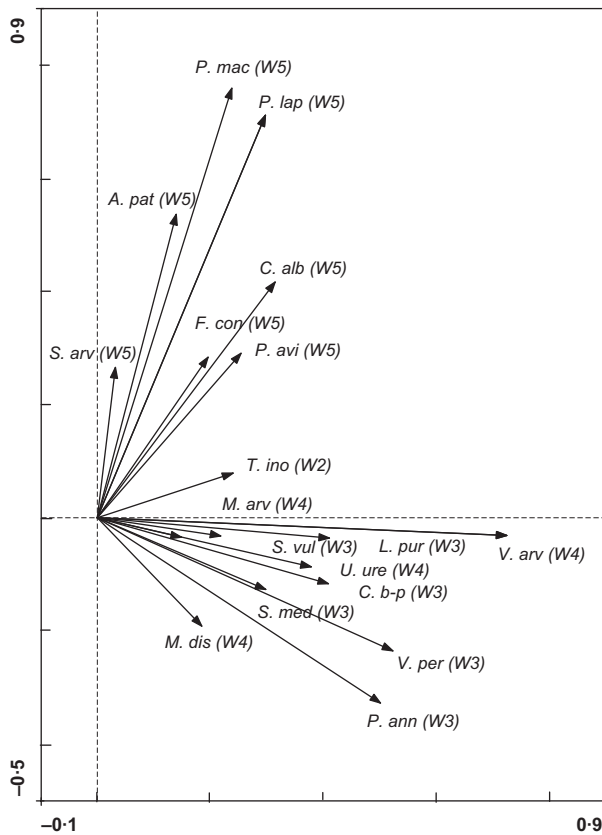
Fig. 1. Partial principal component analysis (pPCA) of emerged weeds, across all crops in the summer, showing species with the strongest fit to the first two axes, after correcting for year, geographical and crop effects. Figures in brackets indicate weed functional groups (see Table 1 for groups and species abbreviations). Seed rain species across all crops and emerged weeds in other data sets have similar ordination patterns (see Fig. S1, Supporting information).

variables describing these distinct communities (Table S1, Supporting information).

INVERTEBRATE PREY EXPLANATORY VARIABLES

All carabids can prey on a wide-range of invertebrates (Sunderland 2002). Therefore, to assess the independence of carabid responses to weeds, we also modelled associations with the majority of their prey, using wide-ranging FSE invertebrate data. Variables were constructed for Collembola, Parasitica, spiders, aphids, Auchenorrhyncha, Heteroptera, Staphylinidae, Diptera and lepidopteron larvae, sampled by combinations of pitfall trapping, Vortis suction sampling or direct counts. Variables for counts of earthworm casts in quadrats and gastropods in baited refuge traps, consisting of large, inverted plastic plant-pot saucers, were also included (see Supporting Information, Table S1 for full descriptions of prey variables and sampling methodology).

CARABID RESPONSE VARIABLES

Carabid variables consisted of total counts from 12 pitfall traps, located on four of the transects used to sample weeds, at 2, 8 and 32 m from the crop edge. Traps were run for 2 week-periods, on three separate occasions, divided between May, July and August for spring crops and late September to October, late April to May and

late June to early July for winter oilseed rape. Data across all crops were divided into sets covering one round of sampling in spring (using April–May traps) and one in summer (using June–July traps). Half-fields were included in analyses when at least 80% of traps were present and comprehensive data for explanatory variables were available, with totals adjusted to account for any missing traps. Variables describing the functional similarity of carabids were formed prior to the analysis by grouping species according to their traits, using relevant literature (Table 2). Taxa were classified as carnivores if only limited evidence of ingestion of plant material could be found, as omnivores with a mixed diet if feeding on seeds and invertebrates was recorded, and as omnivores with a preference for granivory, if a predilection for seeds over invertebrates was demonstrated (see, e.g., Tooley & Brust 2002; Honek *et al.* 2007). Carnivores were included to avoid any erroneous assumptions about functional responses of the whole carabid community. Total abundance of functional groups was modelled using all species. Very rare species, with > 75% of their data comprised of zeros, were dropped from other analyses, leaving species accounting for at least 97% of the total abundance within each group (Table 2).

LINKS BETWEEN FUNCTIONAL GROUPS

Carabids responded strongly to geographical gradients and different crops in the FSE (Brooks *et al.* 2008). To robustly model the wide-scale consistency of carabid trophic responses, we therefore included a baseline component in all models to describe significant spatial, crop and survey year effects. To assess the unified responses of species within functional groups and thereby provide evidence that links are consistent across agglomerations of taxa, symmetric matrices of the distances between half-fields were formed for each of the groups listed in Tables 1 and 2, using counts of their constituent species. Additionally, matrices were calculated to account for geographical distances between half-fields, refined by truncation to their furthest inter-node distance in a Delaunay triangulation network (Borcard & Legendre 2002). Presence–absence matrices were also used to correct for crop and sampling year, together with matrices based on total weed, seed and invertebrate counts. Multiple regressions were performed on these distance matrices according to the methods described by Legendre, Lapointe & Casgrain (1994). This method uses an extension of the Mantel test to compute partial correlation coefficients between multiple matrices and test their significance by repeatedly permuting the rows and columns in the dependent matrix. Separate models were developed for each carabid group, by fitting significant year, crop and geographical matrices. A stepwise procedure was then used to select matrices describing all weed and invertebrate groups with significant additive effects. Matrices were fitted by forward selection and dropped by backwards elimination, according to a predefined Bonferroni corrected *P*-value of 0·05, using a permutation test of their multiple coefficient of determination. Regressions were developed using matrices calculated with four commonly used distance coefficients (Legendre & Gallagher 2001) and the most parsimonious method used to parameterise final models.

The results of the multiple matrix comparisons were corroborated by modelling the links between weeds, invertebrates and carabids using total abundances of their groups. This was done with log-linear regressions using a generalised linear model (GLM) assuming a Poisson distribution for each response and specifying the logarithmic link function to relate the mean response to the linear predictor (McCullagh & Nelder 1989). Multiple regression models were

Table 2. Functional groups of carabid taxa included in multivariate analyses: (C1) small, spring-breeding carnivores; (C2) autumn-breeding carnivores; omnivores with a mixed (M) diet of seeds and invertebrate prey, divided between; (C3) smaller, spring breeders and (C4) larger, autumn breeders; omnivores with preferences for granivory (G), divided between; (C5) smaller, spring breeders and (C6) larger, autumn breeders. The summed abundance across each group is shown for the listed species, together with their percentage coverage of the wider count of all taxa in the respective group. Within groups, taxa are listed by rank abundance, where total counts fall within the ranges: A = 30 001–*c.* 347 000; B = 10 001–30 000; C = 1001–10 000; D = 501–1000 and E ≤ 501

	Abundance		Ecological traits		
Functional group/species	Total	%	Feeding guild	Size: mean (range) in mm	Breeding period
Group C1					
Bembidion lampros (B), *B. tetracolum* (B), *Anchomenus dorsalis* (C), *Notiophilus biguttatus* (C), *B. quadrimaculatum* (C), *B. obtusum* (C), *Loricera pilicornis* (C), *B. guttula* (E), *B. aeneum* (E), *Pterostichus strenuus* (E), *Demetrias atricapillus* (E), *B. lunulatum* (E), *Clivina fossor* (E), *B. properans* (E), *Stomis pumicatus* (E), *Asaphidion flavipes* (E), *P. nigrita* (E), *N. quadripunctatus* (E)	49 203	99·1	Carnivore	5·29 (3·00–10·50)	Spring
Group C2					
Nebria brevicollis (B), *Trechus quadristriatus* (C), *N. salina* (C), *Leistus spinibarbis* (E), *Synuchus vivalis* (E), *Carabus violaceus* (E), *Patrobus atrorufus* (E), *Abax parallelepipedus* (E)	30 396	99·4	Carnivore	12·29 (3·85–25·00)	Autumn
Group C3					
Poecilus cupreus (B) *(P. cup)*, *Agonum muelleri* (D) *(A. meu)*	13 183	99·9	Omnivore-M	10·00 (8·00–12·00)	Spring
Group C4					
Pterostichus melanarius (A) *(P. mel)*, *P. madidus* (A), *P. niger* (B) *(P. nig)*, *Calathus fuscipes* (C) *(C. fus)*, *C. melanocephalus* (C) *(C. mel)*, *C. rotundicollis* (E) *(C. rot)*	491 727	99·9	Omnivore-M	13·04 (7·25–18·50)	Autumn
Group C5					
Amara similata (C) *(A. sim)*, *A. ovata* (D) *(A. ova)*, *A. aenea* (E) *(A. aen)*, *A. plebeja* (E) *(A. ple)*, *A. familiaris* (E) *(A. fam)*	5323	97·4	Omnivore-G	7·69 (6·40–8·75)	Spring
Group C6					
Harpalus rufipes (B) *(H. ruf)*, *Curtonotus aulicus* (E) *(C. aul)*, *Ophonus* spp. (E) *(Oph)*	28 579	99·9	Omnivore-G	11·83 (9·50–13·50)	Autumn
H. affinis (C) *(H. aff)*				10·50	Spring/Autumn

developed for each carabid group by stepwise selection of year, crop and geographical variables to form a baseline component, and additive effects of weed and invertebrate variables were tested after further refinement by stepwise selection; see Table S2 (Supporting information) for a full description of this methodology.

LINKS BETWEEN TAXA

To test the validity of models connecting functional groups, patterns in the trophic relationships of individual taxa were investigated, without prior expectations about how species traits and responses might be linked. Links between carabid communities and multiple weed and invertebrate explanatory variables (Table S1, Supporting information) were modelled with partial redundancy analyses (pRDA) (Ter Braak 1995). Final models were

simplified by forward selection of the explanatory variables and assessed by Monte Carlo permutation tests of canonical axes and retained variables. First, responses of carnivores and omnivores were modelled to investigate how the combined effects of weeds and invertebrates structured the whole carabid community. Second, models were reduced to omnivorous carabids and weed variables. To further investigate trends in pRDAs and their consistency across species, logistic regression modelling was used to test links between taxa traits and their responses to the trophic resource gradients represented by lower canonical axes. This was done by regressing the proportional abundances between individual carabid species and counts of all carabids within samples (half-fields) against correlations of those samples with axes in the pRDA, with an additional interaction term between categorical descriptions of the functional groups of these species and the axes

Table 3. Multiple matrix regression models comparing half-field differences of: species within carabid functional groups (dependent matrix); crops (CR) and geographical locations (GEO) of half-fields (independent baseline model matrices shown in italics), and species within emerged weed or seed rain functional groups, emerged weed and seed rain total counts, families of Collembola or counts of other invertebrate groups (independent, additional model matrices, shown in bold), where COL = Collembola, WOR = earthworms, SPI = spiders, TEW = total emerged weeds and weed seed rain functional groups, shown by W followed by respective group number. Independent parameters are shown with their standardised partial regression coefficients; number and letter suffixes, for baseline and additional terms, respectively, indicate their associated probabilities (*P*), tested by a permutation test (999 randomisations of the rows and columns of dependent matrices), under the null hypothesis of no concordance between matrices. Weed group terms entering final models were derived from seed rain matrices: those describing emerged weed counts of the same group were also significant when substituted in the models, shown by the respective suffix underlined

Carabid functional group/data set	Distance metric	Fitted terms in final model	Baseline model terms *t*-value (d.f.)	*P*	Additional model terms *t*-value (d.f.)	*P*	Fit of final model R^2	*P*
Carabid Group C1								
All crops/spring	Bray-Curtis	*0·206•CR(1)* + *0·223•GEO(2)* + **0·096•COL(a)**	(1) 34·659 $_{(225)}$ (2) 37·116 $_{(225)}$	0·002 0·002	(a) 16·041 $_{(225)}$	0·018	0·111	0·002
All crops/summer	Bray-Curtis	*0·151•CR(1)* + *0·079•GEO(2)* + **0·073•COL(a)**	(1) 24·142 $_{(224)}$ (2) 12·640 $_{(224)}$	0·002 0·020	(a) 11·652 $_{(224)}$	0·028	0·037	0·002
Carabid Group C2								
All crops/spring	Bray-Curtis	*0·040•CR(1)* + **0·115•COL(a)**	(1) 6·320 $_{(225)}$	0·002	(a) 18·398 $_{(225)}$	0·010	0·016	0·008
All crops/summer	Euclidean	*0·120•CR(1)* + *0·127•GEO(2)* + **0·058•WOR(a)**	(1) 19·304 $_{(224)}$ (2) 20·486 $_{(224)}$	0·002 0·004	(a) 9·358 $_{(224)}$	0·012	0·036	0·002
Carabid Group C4								
All crops/spring	Bray-Curtis	*0·053•CR(1)* + *0·106•GEO(2)* + **0·122•SPI(a)** + **0·148•COL(b)**	(1) 8·617 $_{(225)}$ (2) 17·279 $_{(225)}$	0·002 0·008	(a) 19·741 $_{(225)}$ (b) 23·788 $_{(225)}$	0·004 0·006	0·063	0·002
All crops/summer	Bray-Curtis	*0·104•CR(1)* + *0·301•GEO(2)* + **0·106•TEW(a)** + **0·077•W5(b)**	(1) 17·524 $_{(224)}$ (2) 50·941 $_{(224)}$	0·002 0·002	(a) 17·765 $_{(224)}$ (b) 12·967 $_{(224)}$	0·006 0·006	0·134	0·002
Carabid Group C5								
All crops/spring	Bray-Curtis	*0·210•CR(1)* + **0·137•COL(a)**	(1) 34·529 $_{(225)}$	0·002	(a) 22·760 $_{(225)}$	0·002	0·065	0·002
All crops/summer	Euclidean	*0·122•CR(1)* + **0·263•W3(a)**	(1) 20·042 $_{(224)}$	0·002	(a) 43·354 $_{(224)}$ (a) 28·640 $_{(224)}$	0·002 0·002	0·090	0·002
Carabid Group C6								
All crops/spring	Bray-Curtis	*0·143•GEO(1)* + **0·113•COL(a)**	(1) 22·918 $_{(225)}$	0·002	(a) 18·157 $_{(225)}$	0·010	0·038	0·002
All crops/summer	Bray-Curtis	*0·043•CR(1)* + *0·226•GEO(2)* + **0·136•W5(a)**	(1) 6·977 $_{(224)}$ (2) 37·087 $_{(224)}$	0·002 0·002	(a) 22·193 $_{(224)}$ (a) 18·559 $_{(224)}$	0·002 0·004	0·074	0·002

fitted to test whether carabid traits explained significant contrasts in their responses to trophic gradients. Additionally, univariate responses of each carabid species were investigated by the methodology used to model total counts of functional groups. To assess whether any trophic links were because of similarities in the phenology of taxa, splined abundance data of weeds and carabids were plotted against time across the season.

Results

RESPONSES OF THE WHOLE CARABID COMMUNITY

When seeds were unavailable in the early part of the season, all carabids were predominantly associated with invertebrate prey in matrix and log-linear regression analyses (Tables 3 and S2a, Supporting information). Comparisons of distance matrices, derived from multiple taxa, demonstrated the importance of collembolan prey for all carabids at this time (Table 3). Isotomidae and, to a lesser extent, Entomobryidae were particularly important, accounting for over two-thirds of species responses to collembolan families in the spring (Table S3, Supporting information). Forward selection of

variables in a pRDA confirmed the importance of invertebrate prey, especially Collembola, for the whole carabid community at this time (Fig. S2, Supporting information).

With increasing weed seed availability in the summer, carabids diversified their trophic responses and distinct preferences emerged between functional groups. As expected, carnivorous carabids maintained their strong associations with invertebrate prey (Tables 3 and S2a, Supporting information). Abundant, mixed-feeding omnivores (Group C4) retained some associations with invertebrate prey, but weed resources became important for many of these species (Tables 3 and S3, Supporting information). Other omnivores shifted their preferences even more strongly from invertebrates to weeds in the summer (Tables 3, S2a and S3, Supporting information). Multivariate models highlighted these contrasting responses, confirming that invertebrates and weeds were important for structuring the whole community at this time, with Collembola and earthworms particularly important in the ordination of carnivorous species, and weed resources mediating the responses of most omnivores (Fig. S2, Supporting information).
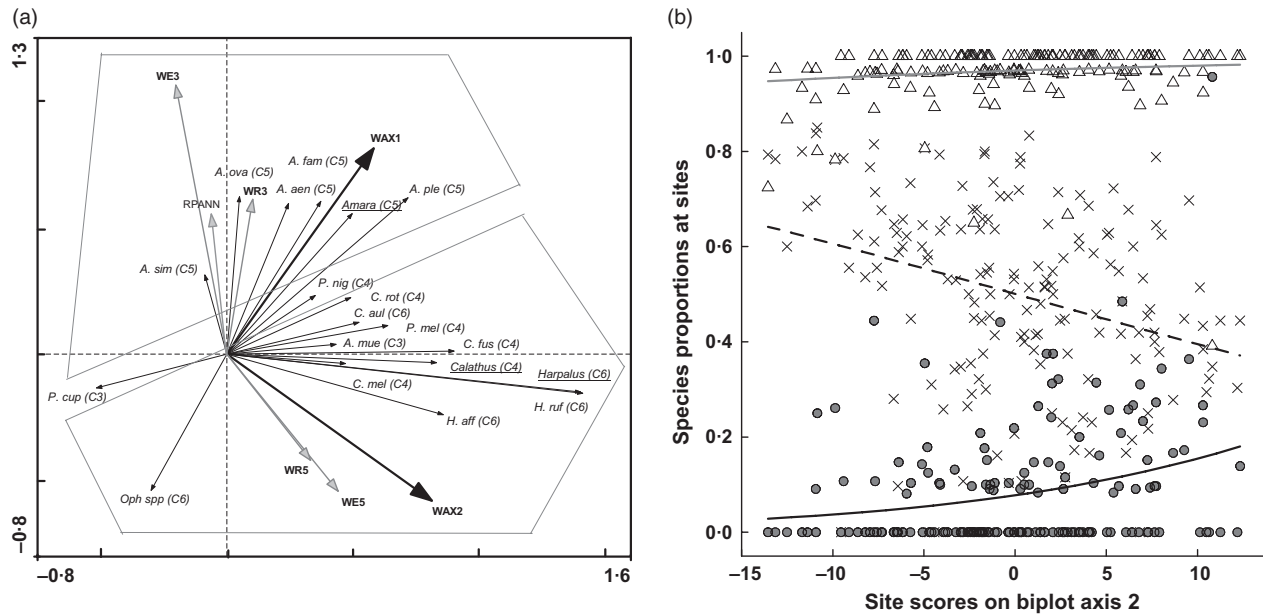
Fig. 2. Omnivorous carabid responses to weeds in spring crops in the summer: (a) partial redundancy analysis (pRDA) of carabid responses; figures in brackets indicate carabid functional groups (see Table 2 for species abbreviations); underlined genera are projected passively onto the diagram; significant explanatory weed variables are shown by bold vectors; WAX1 = PCA axis representing small-seeded weed taxa in Groups W2, W3 and W4 (conditional eigenvalue = 0·012, $F_{(10,154)}$ = 2·68, P = 0·022), and WAX2 = PCA axis for Group W5 weeds (marginal eigenvalue = 0·021, $F_{(9,155)}$ = 4·81, P = 0·004); other explanatory variables are shown by grey line vectors and are projected passively onto the diagram; WE and WR = logit-transformed ratios of emerged weed and seed rain counts, respectively, within the functional group indicated by the proceeding number; RPANN = *Poa annua* seed rain; envelopes contain carabid and weed variables with significant univariate relationships (see Table S3, Supporting information); and (b) logistic regression model, with fitted binomial error structure, where dependent variables are the proportion of counts of each carabid taxa to total carabid counts at sites, categorised by their functional groups; C4 (upward triangles, trend = solid grey line); C5 (circles, trend = solid black line) and C6 (crosses, trend = broken black line) and independent variables are half-field scores on the second axis of the pRDA; the interaction between a factor for carabid groups and the second pRDA axis is significant in an accumulated analysis of variance (deviance ratio $_{(2,489)}$ = 18·29, $P \leq 0.001$); with the parameter for Group C5 being significantly different from Groups C4 and C6 (coefficient = −0·086, t-value$_{(2,489)}$ = −2·81, P = 0·005), a dispersion parameter of 4·23 from the residual deviance was fitted.
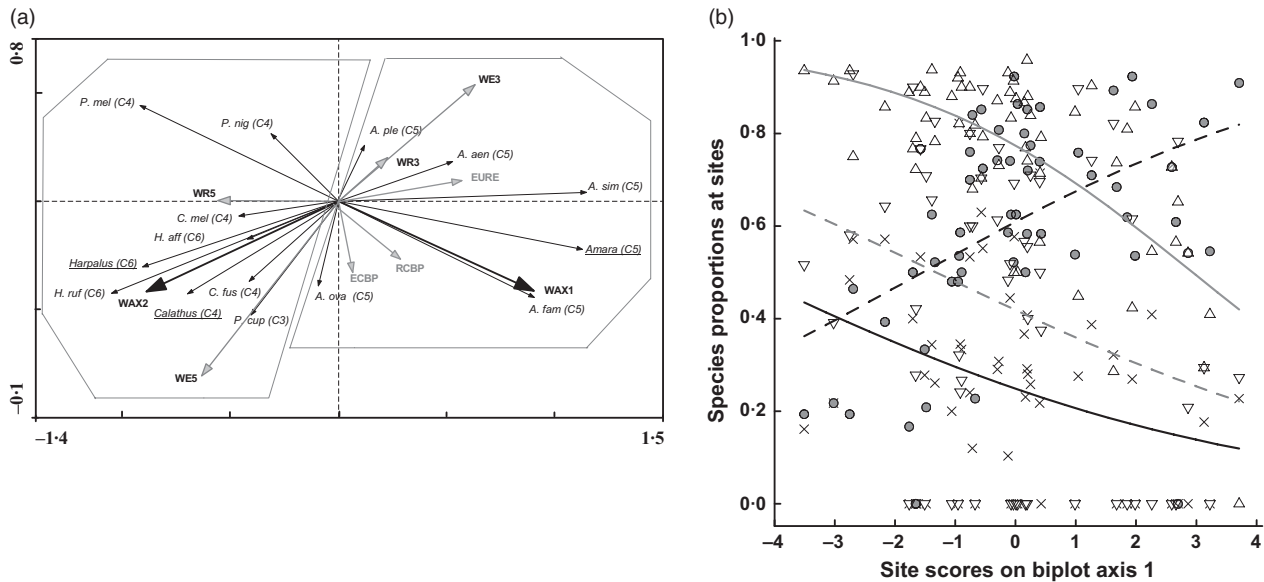
RESPONSES OF OMNIVOROUS CARABIDS

Omnivorous species accounted for around 87% of total carabid abundance (Table 2). Weed seeds were the most valuable food for these carabids during the summer (Tables 3 and S2a, Supporting information), but these resources were not utilised in a uniform way. Preferences of carabid taxa differed markedly according to both their functional grouping and that of the weed community. Autumn-breeding, omnivorous carabids (Group C4) were correlated with total weeds across all crops (Table S2a, Supporting information). However, when the consistency of responses between these taxa was emphasised by matrix regressions and ordinations, there was a preference for spring-germinating weeds in Group W5 (Table 3 and Figs 2a and 3a). Responses of more specialised seed-feeding omnivores became strongly divergent, with contrasting but even stronger links established between weeds in different functional groups. Larger, mainly autumn-breeding carabids (Group C6) were strongly correlated with larger-seeded, spring-germinating weeds in Group W5 (Table S2a, Supporting information). Matrix regression, pRDA ordination and log-linear analyses demonstrated the consistency of such links across species (Tables 3 and S3, Supporting information and Figs 2 and 3). Of the autumn-breeding, omnivorous carabids, *Calathus* and *Harpalus* spp., were noticeable for their consis-

tent and significant relationships with Group W5 weeds (Table S3, Supporting information and Figs 2a and 3a).

In contrast to other omnivorous species, smaller, spring-breeding carabids, with a preference for granivory in Group C5, had exclusive and noticeably uniform responses to small-seeded, autumn-germinating weeds in Groups W2, W3 and W4 (Tables 3, S2a and S3, Supporting information and Figs 2a and 3a). Comparisons between weed matrices and log-linear analyses demonstrated that short, early flowering weeds in Group W3 were most important for Group C5 carabids, as responses were at their strongest and most consistent across taxa in this functional group (Tables 3 and S2). Group W3 weeds were, however, associated with other small-seeded and autumn-germinating, but later flowering weeds in Groups W2 and W4 (Figs 1 and S1, Supporting information). Ordinations revealed close links between Group C5 carabids and community descriptors of weeds sharing these traits (Figs 2a and 3a), and log-linear analyses demonstrated correlations between a number of weed species with these traits in Groups W2/W4 and these beetles (Tables S2a and S3). This suggests that periodicity of emergence and seed size, rather than flowering time, are the main weed traits driving the responses of Group C5 carabids. Like other generalist omnivores, Group C3 carabids had preferences for Group W5 weeds, but the strongest response of the dominant species

Fig. 3. Omnivorous carabid responses to weeds in winter oilseed rape in the spring and early summer: (a) partial redundancy analysis (pRDA) of carabid responses: see Fig. 2 for variable descriptions and diagram formatting, additionally; ECBP and RCBP = emerged and seed rain counts of *Capsella bursa-pastoris*, respectively, and EURE = emerged counts of *Urtica urens*; significant explanatory variables under independent tests; WAX1 (eigenvalue = 0·042, $F_{(6,52)}$ = 4·05, P = 0·002) and WAX2 (eigenvalue = 0·041, $F_{(6,52)}$ = 4·02, P = 0·002); and (b) logistic regression model, see Fig. 2 for descriptions of the symbols, trend lines and parameterisation of the model, additionally; Group C3 carabids are shown by downward triangles and broken grey trend line; the interaction between a factor for carabid groups and the first pRDA axis is significant in an accumulated analysis of variance (deviance ratio $_{(3,228)}$ = 10·71, $P \leq 0.001$); with the parameter for Group C5 being significantly different from Groups C3, C4 and C6 (coefficient = −0·538, t-value$_{(228)}$ = −4·08, $P \leq 0.001$), a dispersion parameter of 7·12 from the residual deviance was fitted.

in the group, *Poecilus cupreus* (Linnaeus), was towards diverse plant communities (Table S3).

The trait-mediated links between trophic levels observed here, as well as being applicable to multiple taxa, are also consistent at wide spatial scales, being robust to ecosystem perturbations caused by changing crops, regions and years (Table S2b). Phenological synchronicity between different weed and carabid functional groups could not account for the quantitative links established between them. Although there were seasonal coincidences in the peaks of trophically associated functional groups, they were not mirrored by concomitant dissimilarities in the actual availability of different seed resources. For example, the abundance of seed rain from Group W3 weeds was always much higher than that of Group W5 in winter oilseed rape, regardless of the phenology of the taxa (Fig. S3, Supporting information).

Discussion

Our results validate the hypothesis postulated by Lavorel & Garnier (2002) that traits determining the response of one group of organisms to the environment can, in turn, mediate effects on other functionally related taxa. Elucidating the form of this functional relationship is regarded as crucial to understanding and managing the impacts of anthropogenic change on ecosystem processes (Loreau *et al.* 2001; Kremen 2005). In a recent review of studies taking a functional trait approach, however, only 2% were applicable to trophic interactions (De Bello *et al.* 2010). Nonetheless, finding the mech-

anisms underlying trophic links is critical for modelling ecosystem dynamics because of cascading and amplification of effects between trophic levels (Thébault & Loreau 2003), which can affect community stability (Ives, Cardinale & Snyder 2005). Our results increase evidence that Lavorel & Garnier's (2002) hypothesis can be extended to trophic systems (Schmitz 2008), particularly as our study additionally shows that it can contain the inherent complexity of multiple, interacting species in diverse plant and insect communities.

More particularly, however, we show that the functional relationships described by Lavorel & Garnier (2002) are applicable not only to trophic interactions but to their robust modelling over wide spatial scales, something that was previously unknown (De Bello *et al.* 2010). This is vital for the wider application of Lavorel & Garnier's (2002) hypothesis because spatial scaling can fundamentally alter the dynamics of trophic links. For example, effects of landscape variation can be compounded through trophic levels, causing higher levels to respond at disproportionately wider spatial scales (Tscharntke & Brandl 2004; Purtauf, Dauber & Wolters 2005). Differences between the responses of carabid trophic groups have also been reported at this spatial scale, with granivores benefiting more from landscape diversity than carnivores (Vanbergen *et al.* 2010). Additionally, how trophically interacting species are linked spatially can determine their wide-scale responses to climate change (Schweiger *et al.* 2008). For our study system, however, we found that within-field variation in weed communities was sufficiently strong and consistent over large spatial scales to drive the wide-scale population dynamics of carabids.

These patterns in weed communities will be a product of the timing of previous cultivations, largely determined by the proportion of spring cropping, and weed control in the current crop (Legere & Samson 1999). This enables a direct link to be made from crop management to carabid communities via plant traits, with autumn-germinating, small-seeded weeds associated with small, spring-breeding carabids, and spring-germinating, mainly large-seeded weeds, associated with larger, autumn-breeding carabids. Our results therefore highlight the utility of functional traits for modelling how the effects of perturbations cascade through trophic levels. More crucially, however, they also show that such functional relationships can be stable across wide gradients of disturbance and spatial variation, in our case caused by contrasting management and cropping regimes, and large-scale, regional differences in biogeography.

The trophic links found may extend the value of carabids as environmental indicators by allowing better predictions of how changes in weed communities influence wider biodiversity. For example, *Amara* spp. may indicate changes beneficial to insects more generally, as the small-seeded weeds that they are associated with provide resources for many phytophagous taxa, whereas *Harpalus* spp. may be good indicators of the availability of larger-seeded weeds, which are important resources for farmland birds (Marshall *et al.* 2003). Corroborating our results in winter cereals would further increase this indicator potential of carabids because these crops account for much wider proportions of the UK landscape than the break crops investigated here. Understanding the mechanisms by which carabids select seeds may also further our understanding of their trophic relationships. Our results are congruent with allometric relationships between the size of carabids and the seeds on which they feed (Honek *et al.* 2007). This alone could explain the preferences of small, spring-breeding carabids which probably have morphological constraints to eating larger seeds. Bigger, autumn-breeding carabids, however, select larger seeds even when they are much less abundant than smaller alternatives, tentatively supporting the theory that unfavoured food for carabids contains toxins limiting consumption rates or that essential nutrients are only supplied by preferred foods (Hendry *et al.* 1994; Toft 1996). Alternatively, selection may be influenced by the timing of cultivations of the crops. For example, many autumn-breeding carabids overwinter as larvae in the soil, and they may have evolved preferences for seeds that germinate better when there is less disturbance at this time.

The viability of many ecosystem processes is rapidly undermined when the most functionally important species decline within a community (Zavaleta & Hulvey 2004; Larsen, Williams & Kremen 2005). Therefore, links between species traits, such those highlighted here, may be useful for predicting and managing these losses in ecosystem function. For example, autumn-breeding, seed-feeding carabids are nearly 100 times more numerous than spring-breeding, seed-feeding carabids, yet their preferred seeds are in much lower supply in some crops than those of the later group. Loss of seeds with traits suitable for autumn-breeding carabids may, therefore, have disproportionately negative effects on the functioning of food webs. Indeed, such trait-mediated responses in plants are often pivotal in how ecosystems function (Tilman *et al.* 1997). Therefore, the approach developed here may have wider potential for modelling the responses of other taxa which rely on weed resources, such as pollinators and phytophagous insects. For example, pollinators can be related to flower traits (Potts *et al.* 2003) and leaf-chewers to leaf traits (Perez-Harguindeguy *et al.* 2003). These trait linkages may provide better quantification of the trade-offs and synergies between resources provided by weeds to different taxa, permitting more comprehensive and integrated modelling of arable plant–invertebrate interactions.

Acknowledgements

References

Borcard, D. & Legendre, P. (2002) All-scale spatial analysis of ecological data by means of principal co-ordinates of neighbour matrices. *Ecological Modelling*, **153**, 51–68.

Brooks, D.R., Perry, J.N., Clark, S.J., Heard, M.S., Firbank, L.G., Holdgate, R., Shortall, C.R., Skellern, M.P. & Woiwod, I.P. (2008) National-scale metacommunity dynamics of carabid beetles in UK farmland. *Journal of Animal Ecology*, **77**, 265–274.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Díaz, S. (2000) Consequences of changing biodiversity. *Nature*, **405**, 234–242.

De Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., Da Silva, P.M., Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., Wardle, D.A. & Harrison, P.A. (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, **19**, 2873–2893.

Firbank, L.G., Heard, M.S., Woiwod, I.P., Hawes, C., Haughton, A.J., Champion, G.T., Scott, R.J., Hill, M.O., Dewar, A.M., Squire, G.R., May, M.J., Brooks, D.R., Bohan, D.A., Daniels, R.E., Osborne, J.L., Roy, D.B., Black, H.I.J., Rothery, P. & Perry, J.N. (2003) An introduction to the Farm-Scale Evaluations of genetically modified herbicide-tolerant crops. *Journal of Applied Ecology*, **40**, 2–16.

Gobbi, M., Caccianiga, M., Cerabolini, F., De Bernardi, F., Luzzaro, A. & Pierce, S. (2010) Plant adaptive responses during primary succession are associated with functional adaptations in ground beetles on deglaciated terrain. *Community Ecology*, **11**, 223–231.

Hendry, G.A.F., Thomson, K., Moss, C.J., Edwards, E. & Thorpe, P.C. (1994) Seed persistence: a correlation between seed longevity in the soil and ortho-dihydroxyphenol concentration. *Functional Ecology*, **8**, 658–664.

Holt, R.D., Grover, J. & Tilman, D. (1994) Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist*, **144**, 741–771.

Honek, A., Martinkova, Z., Saska, P. & Pekar, S. (2007) Size and taxonomic constraints determine the seed preferences of Carabidae (Coleoptera). *Basic and Applied Ecology*, **8**, 343–353.

Ives, A.R., Cardinale, B.J. & Snyder, W.E. (2005) A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning. *Ecology Letters*, **8**, 102–116.

Kremen, C. (2005) Managing ecosystem services: what do we need to know about their ecology? *Ecology Letters*, **8**, 468–479.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vázquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A., Regetz, J. & Ricketts, T.H. (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters*, **10**, 299–314.

Lambeets, K., Vandegehuchte, M.L., Maelfait, J.P. & Bonte, D. (2008) Understanding the impact of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods on river banks. *Journal of Animal Ecology*, **77**, 1162–1174.

Larsen, T.H., Williams, N.M. & Kremen, C. (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, **8**, 538–547.

Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.

Lavorel, S., McIntyre, J., Landsberg, J. & Forbes, T.D.A. (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution*, **12**, 474–478.

Legendre, P. & Gallagher, E.D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271–280.

Legendre, P., Lapointe, F.J. & Casgrain, P. (1994) Modelling brain evolution from behaviour: a permutational regression approach. *Evolution*, **48**, 1487–1499.

Legere, A. & Samson, N. (1999) Relative influence of crop rotation, tillage and weed management on weed associations in spring barley cropping systems. *Weed Science*, **47**, 112–122.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, **294**, 804–808.

Marshall, E.J.P., Brown, V.K., Boatman, N.D., Lutman, P.J.W., Squire, G.R. & Ward, L.K. (2003) The role of weeds in supporting biological diversity within crop fields. *Weed Research*, **43**, 77–89.

May, R.M. (1974) *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, New Jersey, USA.

McCann, K. (2007) Protecting biostructure. *Nature*, **446**, 29.

McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*. Chapman and Hall, London, UK.

Pérez-Harguindeguy, N., Díaz, S., Vendramini, F., Cornelissen, J.H.C., Gurvich, D.E. & Cabido, M. (2003) Leaf traits and herbivore selection in the field and in cafeteria experiments. *Austral Ecology*, **28**, 642–650.

Perry, J.N., Rothery, P., Clark, S.J., Heard, M.S. & Hawes, C. (2003) Design, analysis and statistical power of the Farm-Scale Evaluations of genetically modified herbicide-tolerant crops. *Journal of Applied Ecology*, **40**, 17–31.

Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741–758.

Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G. & Willmer, P. (2003) Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology*, **84**, 2628–2642.

Purtauf, T., Dauber, J. & Wolters, V. (2005) The response of carabids to landscape simplification differs between trophic groups. *Oecologia*, **142**, 458–464.

Purvis, A. & Hector, A. (2000) Getting the measure of biodiversity. *Nature*, **405**, 212–219.

Ribera, I., Dolédec, S., Downie, I.S. & Foster, G.N. (2001) Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology*, **11**, 1112–1129.

Schmitz, O.J. (2008) Effects of predator hunting mode on grassland ecosystem function. *Science*, **319**, 952–954.

Schweiger, O., Settele, J., Kudrna, O., Klotz, S. & Kühn, I. (2008) Climate change can cause spatial mismatch of trophically interacting species. *Ecology*, **89**, 3472–3479.

Simberloff, D. (2004) Community ecology: is it time to move on? *American Naturalist*, **163**, 787–799.

Slansky, F. & Panizzi, A.R. (1986) Nutritional ecology of seed-sucking insects. *Nutritional Ecology of Insects, Mites, Spiders and Related Invertebrates* (eds F. Slansky & J.D. Rodriquez), pp. 283–320, John Wiley and Sons, New York.

Storkey, J. (2006) A functional group approach to the management of UK arable weeds to support biological diversity. *Weed Research*, **46**, 513–522.

Storkey, J., Moss, S.R. & Cussans, J.W. (2010) Using assembly theory to explain changes in a weed flora in response to agricultural intensification. *Weed Science*, **58**, 39–46.

Sunderland, K.D. (2002) Invertebrate pest control by carabids. *The Agroecology of Carabid Beetles* (ed. J.M. Holland), pp. 165–214, Intercept, Andover.

Symstad, A.J., Chapin, F.S., Wall, D.H., Gross, K.L., Huenneke, L.F., Mittlebach, G.G., Peters, D.P.C. & Tilman, D. (2003) Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. *BioScience*, **53**, 89–98.

Ter Braak, C.J.F. (1995) Ordination. *Data Analysis in Community and Landscape Ecology* (eds R.H.G. Longman, C.J.F. ter Braak & O.F.R. Van Tongeren), pp. 91–169, Cambridge University Press, Cambridge.

Ter Braak, C.J.F. & Šmilauer, P. (2002) *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination, version 4.5*. Microcomputer Power, Ithaca, New York.

Thébault, E. & Loreau, M. (2003) Food-web constraints on biodiversity-ecosystem functioning relationships. *Proceedings of the National Academy of Sciences USA*, **100**, 14,949–14,954.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300–1302.

Toft, S. (1996) Indicators of prey quality for arthropod predators. *Arthropod Natural Enemies in Arable Land. II. Survival, Reproduction and Enhancement* (eds C.J.H. Booij & L.J.M.F. den Nijs), pp. 107–116, Åarhus University Press, Åarhus.

Tooley, J. & Brust, G.E. (2002) Weed seed predation by carabid beetles. *The Agroecology of Carabid Beetles* (ed. J.M. Holland), pp. 215–231, Intercept, Andover.

Tscharntke, T. & Brandl, R. (2004) Plant-insect interactions in fragmented landscapes. *Annual Review of Entomology*, **49**, 405–430.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.

Vanbergen, A.J., Woodcock, B.A., Koivula, M., Niemelä, J., Kotze, D.J., Bolger, T., Golden, V., Dubs, F., Boulanger, G., Serrano, J., Lencina, J.L., Serrano, A., Aguiar, C., Gandchamp, A.-C., Stofer, S., Szél, G., Ivits, E., Adler, P., Markus, J. & Watt, A.D. (2010) Trophic level modulates carabid beetle responses to habitat and landscape structure: a pan-European study. *Ecological Entomology*, **35**, 226–235.

Vandewalle, M., De Bello, F., Berg, M.P., Bolger, T., Dolédec, S., Dubs, F., Feld, C.K., Harrington, R., Harrison, P.A., Lavorel, S., Da Silva, P.M., Moretti, M., Niemelä, J., Santos, P., Sattler, T., Sousa, J.P., Sykes, M.T., Vanbergen, A.J. & Woodcock, B.A. (2010) Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation*, **19**, 2921–2947.

Zavaleta, E.S. & Hulvey, K.B. (2004) Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science*, **306**, 1175–1177.

Supporting information

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

Fig. S1. pPCA diagrams of weed community variation.

Fig. S2. pRDA biplots of the response of the whole carabid community to all trophic resources.

Fig. S3. Plots of the seasonal phenology of seed rain and carabid taxa.

Table S1. Descriptions of explanatory variables.

Table S2. (a) Log-linear models linking total counts of invertebrate groups, and functional groups of weeds, to carabids. (b) Full parameterisation of above log-linear models and tests of interactions with baseline terms.

Table S3. Log-linear models of the responses of individual carabid taxa.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.