SPECIAL FEATURE

PLANT FUNCTIONAL EFFECTS ON ECOSYSTEM SERVICES

Using functional traits to quantify the value of plant communities to invertebrate ecosystem service providers in arable landscapes

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Summary

1. The loss of farmland biodiversity threatens the sustainability of ecosystem services delivered within agricultural landscapes. The functional trait approach has been successfully used in grassland systems to quantify trade-offs and synergies between services delivered directly by plant communities. Many of the services delivered by arable landscapes, however, depend on invertebrate consumers, and the application of the trait-based approach to these systems depends on quantifying functional relationships between trophic levels.

2. Two data sets of plant and invertebrate communities from a range of annual crops and uncropped land habitats were analysed. The community-weighted means of plant functional traits were calculated for the vegetation samples and used as the explanatory variables in a multivariate analysis of plant species composition across habitats. The constrained axes scores were used in statistical models to explain the variance in associated total invertebrate abundance, phytophagous invertebrates and invertebrate numbers weighted by importance in the diet of farmland bird chicks.

3. The multivariate analysis discriminated between plant communities characterized by ruderal traits (high specific leaf area and early flowering) and those with more competitive traits. More ruderal communities also supported proportionally more invertebrates. The suite of traits included in the analysis explained a greater proportion of the variance in invertebrate abundance between uncropped habitats, as opposed to between annual crops.

4. The overlap between the plant traits that respond to disturbance (functional response traits) and those that affect the abundance of phytophagous invertebrates (functional effect traits) and the diet of farmland birds demonstrates the potential for using common functional metrics to integrate the assessment of an ecosystem service across different habitats particularly on uncropped land where intensity of disturbance is the main environmental driver.

5. *Synthesis.* The quantification of functional linkages between arable plants and the abundance of their associated invertebrate consumer communities is the first step in extending the trait-based approach to quantify trade-offs and synergies between ecosystem services developed in grassland systems to landscapes dominated by arable crops. However, applying the functional approach to in-crop weed communities and other service providers such as pollinators will require the incorporation of additional response and effect traits.

Key-words: agri-environment schemes, ecosystem services, farmland birds, leaf dry matter content, palatability, plant–herbivore interactions, specific leaf area

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Introduction

The adoption of the concept of ecosystem services within the scientific and environmental policy communities has highlighted a number of systems where current land use policy is unsustainable in terms of balancing the suite of ecosystem services they deliver (Luck *et al.* 2009; Brown *et al.* 2011; Diaz *et al.* 2011). Nowhere is this more apparent than in agricultural landscapes. Farmland is the largest land use type in Europe but reconciling the need for provisioning services of food and energy production with other supporting, regulating or cultural services presents a significant challenge (Zhang *et al.* 2007; Power 2010). The non-provisioning services within agro-ecosystems are largely delivered by non-crop biodiversity that has suffered serious declines over recent decades as a consequence of the intensification of production (Chamberlain *et al.* 2000; Stoate *et al.* 2001; Robinson & Sutherland 2002; Storkey *et al.* 2012). There is concern that the continued degradation of natural capital may threaten sustainable crop production by, for example, adversely affecting pollination services, natural enemy control of pest populations and soil fertility and structure (Kremen 2005).

The use of plant functional diversity metrics to quantify the delivery of ecosystem services and trade-offs between services is increasingly been demonstrated, particularly for primary productivity, support of livestock and nutrient cycling in grassland systems (Vile, Shipley & Garnier 2006; Diaz *et al.* 2007; Lavorel & Grigulis 2012), and there is value in developing similar approaches in arable systems to reconcile conflicting ecosystem services. Non-crop plant communities in arable landscapes deliver a number of ecosystem services directly, including reducing erosion through soil stabilization, nutrient retention, climate regulation and purification of water courses by buffering against diffuse pollution by agrochemicals (Zhang *et al.* 2007). However, much of the focus on ecosystem services in arable systems is on services provided by the consumers of plant resources found in the mosaic of farmland habitats. These include the regulating services of pollination (Lonsdorf *et al.* 2009), biocontrol of crop pests (Bianchi & Wackers 2008), weed seed predation (Bohan *et al.* 2011a) and cultural services including the support of farmland bird populations (Bradbury, Stoate & Tallowin 2010). An extension of the trait-based approach to modelling the impact of change on these services requires the quantification of functional linkages between multiple trophic levels, of which there are relatively few examples in the literature (de Bello *et al.* 2010). Developing quantitative models of the positive contribution made by noncrop plants in arable landscapes will be important for designing sustainable systems that maintain regulating services without compromising the main provisioning service of food, fibre and fuel production.

The interactions between plants and consumers within arable systems have generally been based on qualitative associations between plants and consumers (Wilson *et al.* 1999; Marshall *et al.* 2003; Holland *et al.* 2006) or community approaches using food web algorithms (Bohan *et al.* 2011b;

Pocock, Evans & Memmott 2012). However, recently a number of studies have attempted to identify functional relationships between taxa either using functional groups or characterizing species by their ecological requirements (Storkey 2006; Butler *et al.* 2009; Hawes *et al.* 2009; Brooks *et al.* 2012). By adopting a functional approach, where species are classified according to functional traits, rather than relying on traditional taxonomic definitions, a better assessment of multitrophic system responses to change could potentially be made (Hawes *et al.* 2005). A functional approach not only allows direct evaluation of the effects of change on the functioning of the system, but also avoids the assumptions that all taxonomic units are functionally equivalent and that there is no redundancy in the system (Hawes *et al.* 2009). A natural progression of this work is to develop models based on continuous metrics of functional traits to link management with ecosystem function via trophic interactions that are applicable across contrasting species pools (Lavorel & Grigulis 2012). This functional approach is particularly attractive for the quantification of ecosystem services where service delivery can be independent of the species identity of consumers, such as the example developed in this analysis – the provision of chick food for breeding farmland birds.

The arable landscape is characterized by a range of habitats ranging from regularly cultivated, cropped fields to less intensively managed field margins and areas of uncropped land. These contrasting habitats represent a gradient of disturbance from field centres to margins and boundaries. It would be expected that the floras adapted to these contrasting habitats will exhibit a continuum of functional traits in response to these gradients that represent trade-offs in plant ecological strategy (Grime *et al.* 1997; Westoby 1998; Storkey, Moss & Cussans 2010; Pakeman 2011). As arable landscapes are generally characterized by high fertility, it would be expected that the main contrast would be between ruderal and competitor strategies (sensu Grime 1974). Species found in more disturbed environments will be characterized by ruderal traits including high specific leaf area (SLA), relative growth rate, shorter development times and small seed size (often reflected in the production of large numbers of seed). Land that is no longer regularly cultivated will be expected to have a perennial community of species characterized by taller stature and later flowering. A number of the functional traits that mediate response to disturbance have also been related in the literature to the palatability of plants to invertebrate herbivores – specifically leaf traits associated with the trade-off between resource acquisition and conservation (Perez-Harguindeguy *et al.* 2003). It can be hypothesized therefore that there will be an overlap between the suite of functional traits that respond to disturbance and fertility and those that determine the value of the plant community to invertebrate herbivores (Lavorel & Garnier 2002).

Two large-scale experiments over multiple sites and years, which sampled plant and invertebrate assemblages in arable landscapes in the UK, have recently been completed. The first, the Farm Scale Evaluations (FSE) of genetically

modified herbicide-tolerant crops (Firbank *et al.* 2003), focussed on cropped fields and the second, Farm4Bio (Holland *et al.* 2007), on different areas of uncropped land managed as wildlife habitats. When combined, they represent a unique resource for validating the functional approach to model the management   plant and invertebrate community   ecosystem service pathway within arable landscapes. These data were used to test three hypotheses: (i) within the arable flora, adapted to environments along a gradient of disturbance, trade-offs between ruderal and competitor traits can be identified, (ii) contrasting management in the arable landscape has selected for communities along this trade-off gradient; this selection pressure was expected to be less evident between the annual crops in the FSE than between uncropped habitats in Farm4Bio that have more variation in their levels of disturbance and (iii) these functional gradients effect the abundance of invertebrate consumers used by farmland birds as a resource for brood rearing.

Materials and methods

DATA SETS

The FSE (Firbank *et al.* 2003) was conducted across the UK from 2000 to 2003 on sugar and fodder beet (65 sites), spring oilseed rape (67 sites), forage maize (68 sites) and winter oilseed rape (68 sites). The aim was to investigate the potential impact of the management of genetically modified herbicide-tolerant crops on farmland biodiversity relative to conventional practice (Squire *et al.* 2003). Each field was divided into two halves, and the treatments (GM or Conventional) were randomly allocated to each. Conventional management was monitored, and an audit of all inputs demonstrated consistency with current commercial practice for each crop (Champion *et al.* 2003). The non-crop floras and associated consumer communities were measured using the abundance of all weed species and a wide range of invertebrates. The biomass of weed species was assessed in the month before harvest, in 1×1 m quadrats located at 2 m and 32 m from the crop edge along 12 transects in each half-field. All weeds that were rooted within the quadrat were cut at ground level, sorted into species and oven-dried at 80 °C for 24 h before being weighed (Heard *et al.* 2003). Invertebrates were sampled from the weed vegetation below the crop using a Vortis suction sampler. Samples consisted of five 10-s 'sucks' taken 1 m apart at 2 m and 32 m from the crop edge at each of three locations around each half-field in June and August, giving a total sampled area of 0.09 m² (Haughton *et al.* 2003). For the purposes of this analysis, only data from the conventional half-fields were used, representing the mean weed biomass m⁻² and invertebrate numbers m⁻² at the half-field scale.

The Farm4Bio project was established to quantify the effect of the scale, quality and arrangement of uncropped land on biodiversity in agro-ecosystems (Holland *et al.* 2007). Fourteen farms were chosen in each of two regions in England (south-west and south-east) and a contiguous 100-ha study area within each farm identified. Within the study area of eight farms in each region, wildlife habitats were established on uncropped land at different scales and arrangements. These habitats consisted of four distinct areas with different management: (i) annually established seed mix based on a cereal and a brassica to encourage wild birds (wild bird cover, WBC), (ii) a perennial seed mix to provide flowering resources (floristically enhanced grass,

FEG), (iii) annually established seed mix to encourage food for farmland bird chicks (insect rich cover, IRC) and (iv) natural regeneration of the naturally occurring arable flora (NR). The habitats were sown in 4 years from 2007 to 2010, but 2007 was excluded from this analysis because of very poor plant establishment in that year. In the remaining six farms, two of which were managed organically, no prescriptions were made for the management of uncropped land that was largely made up of 6-m grass buffer strips. The vegetation in each of the four habitats and on equivalent areas of farmer-managed uncropped land was assessed in June/July in each year by recording the presence/absence of all species in 12 0.71 × 0.71 m quadrats positioned along a 100-m transect and estimating total percentage cover. Vortis samples were taken in June/early July using a modified nozzle that was placed over the vegetation and held for 5 s in each of 15 subsampling locations (giving a total sample area of 0.47 m²) positioned along each of the four habitats or equivalent farmer-managed uncropped land.

SELECTION OF TRAITS

Plant functional traits were selected for the analysis based on the literature of functional responses to management in agricultural systems and links with consumers identified in the literature (Hawes *et al.* 2009; Pakeman 2011; Brooks *et al.* 2012):

1 Number of cotyledons (monocots = 1 and dicots = 0); monocots and dicots have different effect traits (structure and resource quality) and different responses to management (Heard *et al.* 2003).

2 Annuality and life-form (annuals = 0, herbaceous perennials = 0.333, rhizomatous perennials = 0.667 and woody perennials = 1).

3 Development rate (month of first flowering).

4 Duration of flowering (in months); both timing and duration of flowering affect a plant's response to the timing and frequency of disturbance and determine the phasing and quality of resources available to higher trophic levels.

5 Specific leaf area (SLA mm² mg⁻¹).

6 Leaf dry matter content (LDMC, mg g⁻¹).

7 Ln seed mass, which affects fecundity and ability to compete with established vegetation.

8 Maximum height (cm) as an approximation for plant architecture, shade tolerance and apparency to herbivores.

An upper limit to maximum height was set at 200 cm to allow the inclusion of trees and shrubs in the analysis, which were often present in the data bases as seedlings. Values for all traits were obtained for all species identified across both data sets. The values for SLA and LDMC were obtained from the LEDA trait data base (Kleyer *et al.* 2008), seed weight from the seed data base held at Kew gardens, UK (Flynn, Turner & Dickie 2004), and the remaining traits from the Ecoflora data base (Fitter & Peat 1994) supplemented by Clapham, Tutin & Moore (1989).

STATISTICAL ANALYSIS

The matrix of species x the eight traits was first analysed to identify trade-offs between traits in the UK arable flora and to test the hypothesis that species in the data base represent a spectrum of plant ecological strategies from more ruderal to more competitive. Variance in trait values between species were standardized to zero mean and unit standard deviation to give them all equal weight in the analysis before performing a Principal Components Analysis (PCA), using the CANOCO V4.5

program (Ter Braak & Šmilauer 2002); the trait values were used as the 'species' data. For the purposes of this study, it was assumed that the differences in functional effect traits on invertebrate abundance were mediated through the mean traits in the community as opposed to the range of traits (Violle *et al.* 2007; Lavorel & Grigulis 2012). For each vegetation sample in the two data sets, the community-weighted mean for the eight traits was calculated using the relative biomass of the component species in the community. In the case of the Farm4Bio samples, a measure of relative abundance was calculated as the number of quadrats, in which a species was recorded divided by the total number of records of all species along a given transect. Although this could not be regarded as a direct proxy for relative biomass (which would have been a preferable measure for the analysis), it was effective in identifying the dominant species in each sample.

To test the second hypothesis that contrasting management (different crop type in the FSE or habitat in Farm4Bio) had selected for plant communities along this gradient of plant strategy, a Canonical Correspondence Analysis (CCA) was performed on the raw data sets of field-scale species biomass, in each data set separately, using the CANOCO V4.5 program (after first performing a DCA to quantify the length of gradient and confirm that a unimodal model was appropriate). The analysis was constrained using the community-weighted mean values of the eight traits for each of the samples and the significance of the first two axes tested using a permutation test. Forward selection was used to identify the traits that explained the most variance between the samples. Habitat type was included as a supplementary environmental variable and projected passively onto the ordination space.

The PCA analysis of the arable plant trait data base identified strong colinearity between several traits including a negative correlation between SLA and LDMC and time to first flowering and duration of flowering. Rather than attempt to quantify relationships between invertebrate abundance and individual traits, therefore, to test the third hypothesis (that invertebrate abundance responded to variance in the functional composition of plant communities), models were run using the axes scores from the CCA analysis as the explanatory variables. In this way, the effect of contrasts between samples in suites of correlated traits on invertebrate communities was tested. The method of Residual Maximum Likelihood (REML), using GENSTAT 14 (Payne, Murray & Harding 2011), was used to fit a linear mixed model to three response variables for each data set separately: (i) total invertebrate abundance, (ii) abundance of phytophagous invertebrates (excluding predators and detritivores) and (iii) abundance of invertebrates weighted by importance in the diets of a selection of farmland bird chicks. In each case, region and year were considered as random effects and the first and second CCA axes scores as fixed terms. A natural logarithm transformation was applied to the response variables to ensure a normal distribution. To calculate the third response variable, the numbers of individuals in different orders of invertebrates were multiplied by a conversion factor generated from a review of invertebrates as food for farmland birds in Europe (Holland *et al.* 2006). The review paper calculated a mean percentage of the invertebrate chick food diet from a range of sampling methods and composition measures (i.e. percentage of items, percentage biomass and percentage occurrence) for each of 14 farmland bird species; the conversion factor used in this study was calculated as the mean of this variable for all bird species, in which it was present in the diet. It has been established previously that the abundance of consumers is related to plant biomass in arable fields (Haughton *et al.* 2003). Because the aim of this analysis was to quantify qualitative differences in the value of plant resources, all response variables were divided by plant biomass (FSE) or percentage cover (Farm4Bio) before being used in models.

Results

The PCA of variance in trait values between species within the arable flora sampled across both data sets (Fig. 1) confirmed a trade-off between ruderal traits, which increase fitness in disturbed environments (high SLA, frequent and early flowering, and low seed mass) and competitive traits (including tall stature and perennial life-form). There were clear functional trends between the plant communities sampled from different habitats (Table 1). Weed communities sampled from the annual crops in the FSE experiment were characterized by high proportions of annuals with high community-weighted means for ruderal traits (including high SLA and low LDMC). Plant communities sampled from the regularly disturbed habitats in the Farm4Bio experiment had similar trait values to the annual crops. In contrast, the two perennial habitats, floristically enhanced margins and grass margins, had lower SLA, higher LDMC and later flowering.

For both the data sets derived from in-field habitats (FSE) and uncropped land (Farm4Bio), the community-weighted mean values for the eight traits significantly explained a proportion of the variance between plant communities in the CCAs (3.7%, $P = 0.001$ and 8.4%, $P = 0.001$ respectively, Fig. 2). In the case of the Farm4Bio data, where there was a clear distinction between disturbed and undisturbed habitats, the first axis differentiated between samples along the ruderal vs. competitive functional gradient with NR, IRC and WBC (the three annually disturbed habitats) samples associated with high SLA, low LDMC and early and precocious flowering. In contrast, the eight traits explained less of the variance between samples in the FSE data set. The first axis was largely determined by life-form (identified as the most important variable by forward selection), with maize having a higher proportion of perennials (Table 1). However, the second CCA axis reflected the trade-off between communities characterized by more ruderal vs. more competitive traits as was observed in the Farm4Bio data, although this trend does not appear to have been driven by crop types, which were mostly associated with the first axis.

In the Farm4Bio data set, variance in invertebrate abundance per unit cover between samples was correlated with the first CCA axis, with high loadings for SLA, LDMC and flowering time (Table 2, Fig. 3). Although a similar positive relationship between invertebrate abundance per unit weed biomass and these traits was observed in the FSE data set (represented by the second CCA axis), particularly for total invertebrates, a greater proportion of the variance was explained by the first axis, with a high loading for life-form (Table 2). In the Farm4Bio data set, variance in phytophagous invertebrates and invertebrate samples weighted by importance in the diets of farmland bird chicks were similar to those for total invertebrates. However, because of the high proportion of Collembola in the FSE samples, Table 3, variance in total invertebrates was less well correlated with phytophagous invertebrates and chickfood items (Fig. 4).
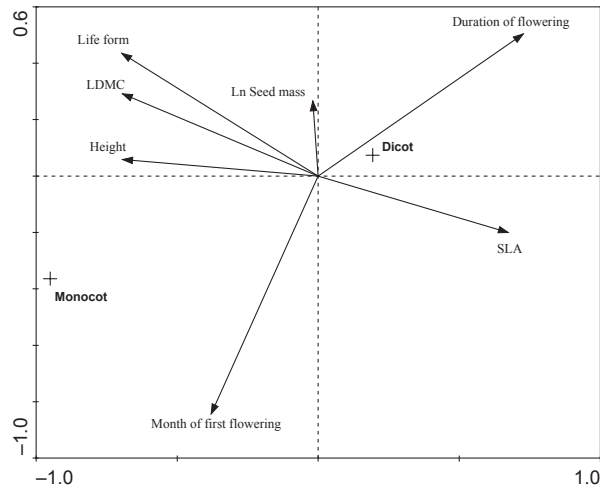
Fig. 1. Trait space occupied by all 432 species represented in any of the habitats sampled in the data bases used in this study represented by a Principal Components Analysis using trait values standardized to zero mean and unit standard deviation. Percentage variance accounted for first two axes = 52.4%. Primary axis represents trade-off between ruderal traits (annuality, high specific leaf area, early, fast development and polycarpy) and competitive traits (perennial life-forms, tall stature and high leaf dry matter content). Trait values and axis scores for all species appear in Appendix S1 (Supporting Information).

Discussion

The plant response/effect framework has proved to be an effective tool for modelling the impact of environmental change on ecosystem services delivered by plant communities, particularly in grassland systems (Lavorel & Grigulis 2012). A natural progression of this approach is to develop quantitative models that incorporate the functional responses of consumers and the ecosystem services they deliver based on their functional response to variance in plant traits. This will be particularly important for extending the trait-based approach to quantifying ecosystem services to arable systems where many services are delivered by consumers. The consistent trend, in both the ordinations of the data base of arable plant traits and the plant communities sampled in the two data sets, between suites of traits that are indicative of ruderal vs. competitive strategies confirmed that frequency of disturbance is an important driver of community assembly in the arable systems analysed in this study. In the Farm4Bio data set, there was a clear functional distinction between habitats with annual disturbance and perennial habitats, reflected by the first CCA axis being driven by ruderal traits including SLA, LDMC and time of flowering. In the FSE data set, where the frequency of disturbance was similar across the crop types, the traits included in this analysis explained less of the variance between fields, where weed communities were largely associated with the specific management of the different crops. The primary ordination axis was driven by the higher proportion of perennial species in the maize plots, possibly as a result of maize often being incorporated into

Table 1. Average community-weighted mean values for eight functional traits (with standard errors in parentheses) calculated for 336 field margin samples in the Farm4Bio data set across five habitat types [natural regeneration (NR), wild bird cover (WBC), insect rich cover (IRC), floristically enhanced grass (FEG) and grass buffer strips (GBS)] and 252 field samples in the FSE data set across four crop types [beet (B), maize (M), spring oilseed rape (SOSR) and winter oilseed rape (WOSR)]

| Trait	B	M	SOSR	WOSR	NR	IRC	WBC	FEG	GBS
Phylogeny	0.19 (0.025)	0.32 (0.043)	0.21 (0.027)	0.26 (0.031)	0.25 (0.025)	0.24 (0.024)	0.19 (0.017)	0.42 (0.016)	0.58 (0.013)
Life-form	0.10 (0.013)	0.21 (0.028)	0.07 (0.014)	0.08 (0.013)	0.17 (0.016)	0.09 (0.011)	0.09 (0.007)	0.39 (0.013)	0.35 (0.008)
First flowering	5.37 (0.141)	5.37 (0.174)	4.97 (0.158)	4.25 (0.160)	4.92 (0.081)	4.87 (0.085)	4.75 (0.103)	5.62 (0.042)	5.37 (0.028)
Flowering duration	5.34 (0.192)	5.04 (0.272)	5.80 (0.245)	6.33 (0.284)	5.45 (0.147)	5.39 (0.149)	5.83 (0.172)	3.79 (0.077)	4.00 (0.055)
SLA	25.75 (0.491)	25.62 (0.621)	28.36 (0.561)	29.36 (0.590)	27.61 (0.272)	26.60 (0.311)	28.17 (0.331)	24.30 (0.172)	25.82 (0.115)
LDMC	181.19 (3.170)	187.32 (4.781)	179.87 (3.849)	172.42 (4.417)	173.66 (3.474)	174.79 (3.697)	161.12 (2.818)	218.27 (2.018)	226.67 (1.391)
Ln seed mass	0.07 (0.072)	0.04 (0.098)	−0.08 (0.068)	−0.34 (0.097)	−0.01 (0.090)	0.46 (0.117)	0.24 (0.100)	−.19 (0.067)	0.13 (0.039)
Height	95.87 (3.832)	88.49 (3.460)	93.92 (3.475)	70.84 (2.310)	91.89 (2.251)	89.67 (1.389)	87.19 (1.934)	84.24 (2.204)	97.56 (1.123)
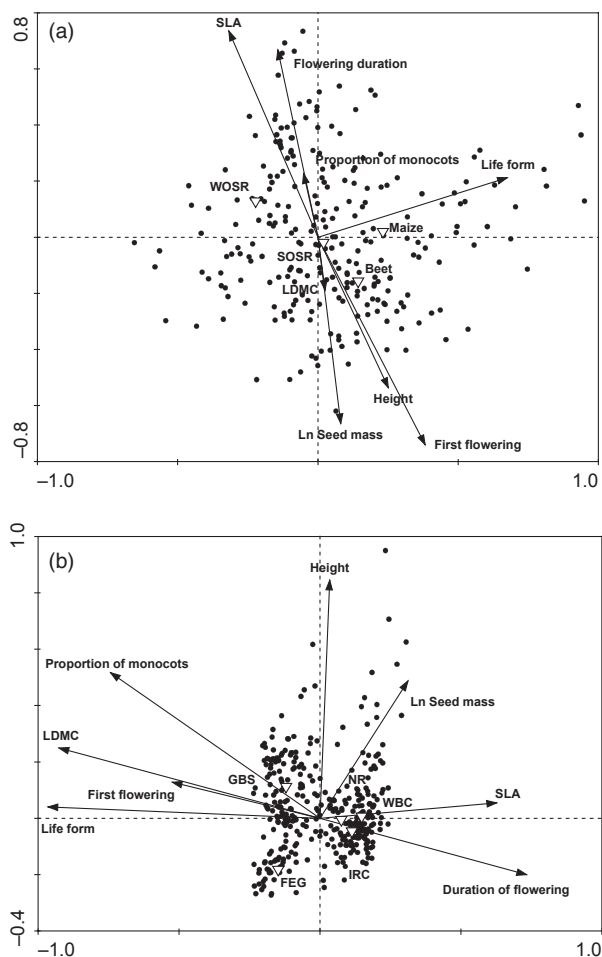
Fig. 2. Canonical Correspondence Analysis for (a) FSE data bases representing a range of annual crops with community-weighted mean values for eight traits for the plant communities in the samples used as explanatory variables. Crop type has been passively projected onto the ordination space. (b) Farm4Bio data with habitat type passively projected: GBS = grass buffer strips, FEG = floristically enhanced grass, WBC = wild bird cover, IRC = insect rich cover, NR = natural regeneration.

a mixed farming system. Despite this, the ruderal/competitive trade-off was still observed on the second ordination axis, possibly as a result of previous field history or the nature of

the margin bordering the crops [the majority of weeds are found on the edges of field and often reflect the flora in the field margins (Marshall 1989)].

Leaf traits can account for the variation in palatability between species (Perez-Harguindeguy *et al.* 2003) and were therefore expected to be a useful common metric for integrating across habitats with contrasting plant communities in terms of their value to invertebrates. The strong positive relationship between the functional axis of SLA vs. LDMC and duration vs. time to first flowering and invertebrate abundance in the Farm4Bio data confirmed that invertebrates were favouring more ruderal communities, the high R^2 for the model indicating a strong overlap between response and effect traits in this data set. Although a similar relationship was observed in the FSE data, invertebrate abundance also appeared to be responding positively to life-form; this is contrary to what would be expected as perennials were generally characterized by a lower SLA and higher LDMC in the trait data base. It is probable that weed community assembly between the different crops is being driven by additional plant traits that have not been included in this analysis, including response to herbicides (Fried, Norton & Reboud 2008; Fried, Chauvel & Reboud 2009). The lower explanatory power of the models in predicting both the functional response of the weed communities to management and the effect on invertebrate abundance suggests that the selection of traits could be improved to better take account of these crop management drivers.

It was expected that the response of phytophagous invertebrate groups to leaf traits would be stronger than that for total invertebrate numbers. However, this effect was not observed and may reflect the complex interactions at the trophic levels above the predators acting as a top down control on herbivore numbers (Hawes *et al.* 2009). However, the fact that variation in the abundance phytophagous invertebrate groups could be modelled using plant functional traits is an important link in the pathway being developed in this study as, in the FSE data set, phytophages were more closely correlated with the dietary requirements of farmland birds.

Non-crop arable plants have traditionally been viewed negatively as an impediment to crop production, reducing yield

Table 2. Relationships between Canonical Correspondence Analysis axis scores constrained by plant traits and invertebrates (per unit weed biomass or percentage plant cover) using a REML analysis with region and year included as random effects and a natural logarithm transformation of the response variables. Axis 2 was not significant in explaining variance in any of the response variables in the Farm4Bio data set and has been excluded from the model.

| Data set	Response variable	Explanatory variable	Estimate (SE)	$F_{(d.f.)}$	F pr.	R^2
Annual crops (FSE)	Total invertebrates	Axis 1 + Axis 2	0.3898 (0.07752)	$22.9_{(244)}$	< 0.001	0.25
			0.1839 (0.08143)	$5.1_{(244)}$	0.025	
	Phytophagous invertebrates	Axis 1 + Axis 2	0.4336 (0.07588)	$30.3_{(244)}$	< 0.001	0.23
			0.1574 (0.07938)	$3.9_{(244)}$	0.048	
	Chick food	Axis 1 + Axis 2	0.4217 (0.07493)	$22.5_{(244)}$	< 0.001	0.23
			0.1483 (0.07824)	$3.6_{(244)}$	0.059	
Uncropped land (Farm4Bio)	Total invertebrates	Axis 1	0.4348 (0.03773)	$132.8_{(303)}$	< 0.001	0.45
	Phytophagous invertebrates	Axis 1	0.4330 (0.03878)	$124.7_{(303)}$	< 0.001	0.44
	Chick food	Axis 1	0.4545 (0.03902)	$135.7_{(303)}$	< 0.001	0.41
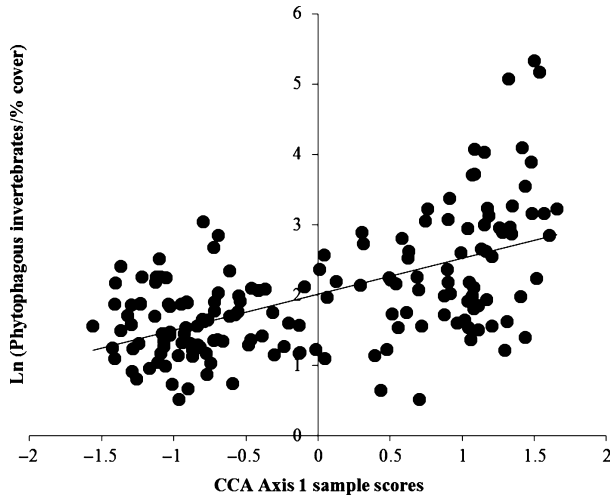
Fig. 3. Relationship between first Canonical Correspondence Analysis axis scores for Farm4Bio samples and invertebrate abundance corrected for plant cover.

Table 3. Summary of the importance of invertebrate orders in the diet of a selection of farmland bird chicks (after Holland *et al.* 2006) and the proportional representation in the two data sets analysed. Data on the diets of 14 farmland bird species were included: skylark, rook, corn bunting, cirl bunting, reed bunting, yellow hammer, chaffinch, house sparrow, linnet, wood pigeon, stone curlew, partridge, red-legged partridge and quail

| Invertebrates	Number of bird species	Mean proportion of diet	Proportion in FSE samples	Proportion in Farm4Bio samples
Acari	1	13	0	0
Amphipoda	1	28	0	0
Arachnida	11	16	0.03	0.04
Cladocera	1	30	0	0
Coleoptera	12	15	0.08	0.11
Coleoptera (L)	7	8	0.01	0.01
Collembola	3	5	0.40	0
Dermaptera	3	5	0	0
Diptera	11	18	0.15	0.27
Diptera (L)	6	9	0.16	0
Errantia	1	38	0	0
Ephemeroptera	1	6	0	0
Hemiptera	9	9	0.09	0.24
Hemiptera (L)	1	2	0	0
Hymenoptera	6	8	0.07	0.32
Isopoda	3	6	0	0
Lepidoptera	5	22	0	0.01
Lepidoptera (L)	7	19	0.01	0
Lumbricidae	5	31	0	0
Neuroptera	1	3	0	0
Orthoptera	5	12	0	0
Plecoptera	1	4	0	0
Pulmonata	2	2	0	0
Symphyta	5	5	0	0
Symphyta (L)	8	13	0	0
Trichoptera	2	4	0	0

L, Larvae.
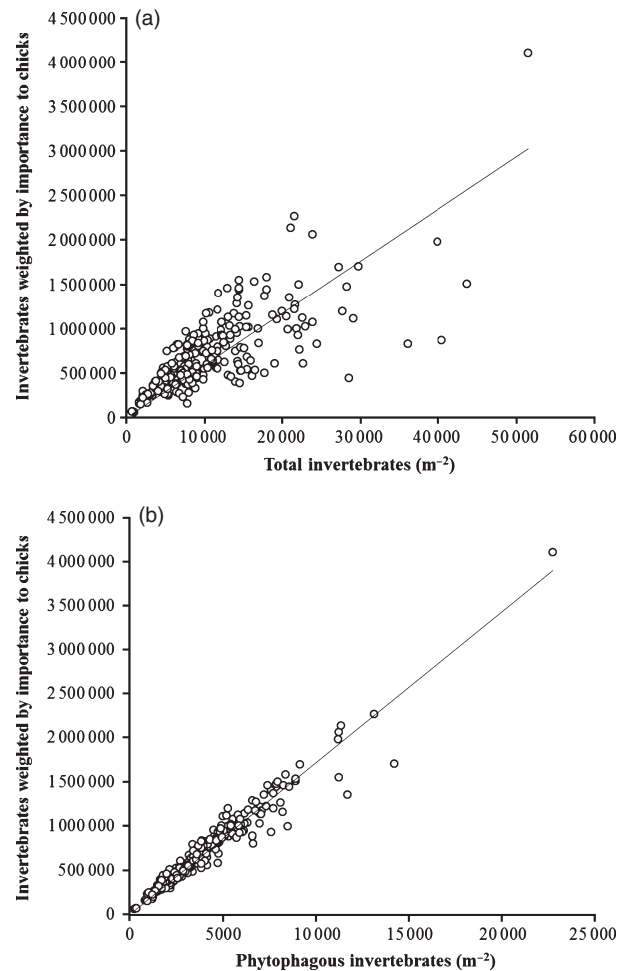
Fig. 4. Correlations between invertebrates weighted by importance in the diet of chicks of a range of farmland birds and (a) total invertebrates and (b) phytophagous invertebrates in the FSE dataset.

and crop quality. Any methodology for quantifying the positive contribution of these floras to maintaining biodiversity and ecosystem services must therefore be set in the context of these dis-services associated with weeds. Because of the negative impact of weeds in crops, the tendency has been to manage plants for conserving ecosystem services, such as farmland birds and pollinators, on uncropped land outside the crop. Within these areas, habitats that require annual establishment are also less favoured by farmers and instead there had been a widespread adoption of perennial habitats with low disturbance such as grass buffer strips (Butler, Vickery & Norris 2007). Our results have demonstrated that a given gram of plant biomass in different habitats is not functionally equivalent and that, in the case of invertebrate food for farmland birds, plant communities adapted to regularly disturbed habitats (ruderals) are preferred over later successional communities. This has implications for the land sparing approach which assumes that field centres will be managed solely for food production. If the function of the weed communities adapted to cultivated fields is to be provided on uncropped land, areas need to be regularly disturbed to encourage desirable ruderal plants (Storkey & Westbury 2007; Westbury

et al. 2008). The analysis of the Farm4Bio data set in this study highlighted the value of wild bird cover, insect rich cover and natural regeneration as example habitats. For the former two, it was the understorey of weeds that provided much of the benefit for invertebrates as opposed to the sown species. However, in the design of the spatial arrangement of these habitats, reference should be made to the ecology of the farmland birds using them as a resource in terms of their foraging behaviour (Butler *et al.* 2009; Henderson *et al.* 2012).

The quantitative relationships between management, plant functional traits and invertebrates that provide an ecosystem service has established a baseline for building a more complex model incorporating different invertebrate functional groups and ecosystem services. Examples include pollinators and biocontrol agents. It is probable that these groups will respond to different plant traits, as already demonstrated for granivorous carabids (Brooks *et al.* 2012). For example, we would expect pollinator abundance to be related to flowering time and nectar quality and quantity. The large data sets used to validate the approach taken in this study have the potential to populate these models with data from sites with contrasting management and environmental variables. These data could be used in the future to build a fully quantified framework of the response of ecosystem services to plant traits to allow multiple services to be mapped at the landscape scale using common functional metrics.

Acknowledgements

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Supporting Information

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

Appendix S1. Table of values for eight functional traits and first axis scores from the PCA analysis for the combined species lists from the FSE and Farm4Bio datasets.