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Response of farmland biodiversity to the introduction of bioenergy crops: effects of local factors and surrounding landscape context

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Abstract

The recent growth in bioenergy crop cultivation, stimulated by the need to implement measures to reduce net CO₂ emissions, is driving major land-use changes with consequences for biodiversity and ecosystem service provision. Although the type of bioenergy crop and its associated management is likely to affect biodiversity at the local (field) scale, landscape context and its interaction with crop type may also influence biodiversity on farms. In this study, we assessed the impact of replacing conventional agricultural crops with two model bioenergy crops (either oilseed rape *Brassica napus* or *Miscanthus* × *giganteus*) on vascular plant, bumblebee, solitary bee, hoverfly and carabid beetle richness, diversity and abundance in 50 sites in Ireland. We assessed whether within-field biodiversity was also related to surrounding landscape structure. We found that local- and landscape-scale variables correlated with biodiversity in these agricultural landscapes. Overall, the differences between the bioenergy crops and the conventional crops on farmland biodiversity were mostly positive (e.g. higher vascular plant richness in *Miscanthus* planted on former conventional tillage, higher solitary bee abundance and richness in *Miscanthus* and oilseed rape compared with conventional crops) or neutral (e.g. no differences between crop types for hoverflies and bumblebees). We showed that these crop type effects were independent of (i.e. no interactions with) the surrounding landscape composition and configuration. However, surrounding landscape context did relate to biodiversity in these farms, negatively for carabid beetles and positively for hoverflies. Although we conclude that the bioenergy crops compared favourably with conventional crops in terms of biodiversity of the taxa studied at the field scale, the effects of large-scale planting in these landscapes could result in very different impacts. Maintaining ecosystem functioning and the delivery of ecosystem services will require a greater understanding of impacts at the landscape scale to ensure the sustainable development of climate change mitigation measures.

Keywords: biodiversity, bioenergy crops, *Brassica napus*, climate change mitigation measures, edge density, grasslands, landscape composition, landscape configuration, *Miscanthus* × *giganteus*, model averaging, seminatural habitats

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Introduction

Changes in land-use as a result of the expansion of the bioenergy sector have the potential to influence biodiversity, which is already declining due to agricultural intensification (Henle *et al.*, 2008; Stoate *et al.*, 2009; Tschamntke *et al.*, 2012). However, the size and direction of the impact that bioenergy crops will have on biodiversity and ecosystem services in agricultural landscapes is not certain (Valentine *et al.*, 2012), and will

depend on the types of crops that are cultivated, the extent and spatial layout of planting in the landscape, what land-use they replace and the management these crops require (Baum *et al.*, 2009; Eggers *et al.*, 2009; Gevers *et al.*, 2011). Unfortunately, the speed at which the bioenergy sector has been developed has left little time for the environmental impact of these various cropping systems to be fully understood (Rowe *et al.*, 2009; Donnelly *et al.*, 2011; Jørgensen, 2011). In addition, as agriculture is projected to contribute much of the potential increase in bioenergy production between now and 2030 (EEA, 2006), it is more critical than ever that we gain a greater understanding of the potential conflicts

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between biodiversity conservation and bioenergy policy objectives to ensure the development of sustainable bioenergy production in agricultural landscapes.

EU member states have set significant renewable energy targets: 20% of energy and 10% of transport fuel are to come from renewable energy by 2020 (Directive 2009/28/EC); and states will in part achieve these targets by planting different combinations of first- and second-generation bioenergy crops on agricultural land. In Ireland, both conventional grassland (typically dominated by perennial ryegrass (*Lolium perenne* L.) and used for silage and intensive dairy/beef production) and tillage crops are being replaced by the perennial rhizomatous grass *Miscanthus* × *giganteus*. Commercial planting of *Miscanthus* began in 2006 with just over 3 000 ha planted to date (SEAI, 2012), actively promoted through establishment grants to farmers (Department of Agriculture, Fisheries & Food, 2010). In addition, large increases in the planting of oilseed rape (*Brassica napus* L.) have occurred in recent years with over 14 000 ha currently in production, representing a substantial shift from food to energy production (Teagasc, 2012).

It is hypothesized that growing perennial crops such as *Miscanthus* should be beneficial for biodiversity when compared with intensively managed annual tillage crops such as oilseed rape and winter wheat, as perennial crops have longer rotation periods, low fertilizer and pesticide requirements, provide better soil protection, offer greater within habitat spatial heterogeneity, have fewer disturbances during the growing season and are harvested during the winter (Lewandowski *et al.*, 2003; EEA, 2007; Heaton *et al.*, 2008; Hastings *et al.*, 2009; Haughton *et al.*, 2009; Rowe *et al.*, 2009). However, although the oilseed rape management regime may have negative effects on biodiversity, it does provide a mass flowering resource and may harbour higher pest densities, which may be beneficial for some pollinating insects and natural enemies (Jauker *et al.*, 2012). Some evidence for the effects of bioenergy crops on biodiversity was provided in a recent review by Dauber *et al.* (2010), who showed that biomass crops in general had positive effects on the species richness of a wide range of taxa when compared with tillage crops at the field scale. However, limited numbers of studies have specifically quantified the impacts of planting *Miscanthus* on biodiversity, with most studies focused on birds and mammals, and few on providers of key ecosystem services to agricultural productivity such as plants, pollinators and natural enemies (Semere & Slater, 2007a,b; Dauber *et al.*, 2010; Stanley & Stout, 2013). Furthermore, few studies have made the necessary comparisons between *Miscanthus* and alternative energy crops (e.g. oilseed rape) or the crops they are likely to replace (e.g. improved grassland, winter wheat) in agricultural landscapes (Bellamy

et al., 2009; Felten & Emmerling, 2011), or on full-scale commercial farms (Dauber *et al.*, 2010).

It is increasingly recognized that the potential effects of agriculture and land-use change on the conservation of biodiversity, and the consequences for ecosystem functioning and services delivery, need a landscape perspective (Loreau *et al.*, 2003; Tschardtke *et al.*, 2005; Macfadyen *et al.*, 2012). In agricultural landscapes, biodiversity not only responds to local-scale management practices in individual fields (e.g. crop type, fertilizer and pesticide use) but also experiences their environment across a broad range of spatial scales (Holzschuh *et al.*, 2007; Batáry *et al.*, 2012; Diaz-Forero *et al.*, 2012). Relationships between higher coverage of seminatural habitats and higher biodiversity are well established (Aviron *et al.*, 2005; Tschardtke *et al.*, 2005; Billeter *et al.*, 2008). However, continuing agricultural intensification, due to growing demands for food and energy production, is increasingly responsible for the structural simplification of agricultural landscapes, resulting in the loss of seminatural habitats and hedgerows, increased use of more intensive and specialized cropping systems, and the creation of larger fields (Firbank *et al.*, 2008). Potential surrounding landscape effects are therefore dependent on compositional heterogeneity (number of land-use/habitat components in the landscape and their relative proportions) and configurational heterogeneity (spatial pattern of the landscape) (Fahrig *et al.*, 2011; Flick *et al.*, 2012). It is hypothesized that landscapes with higher compositional heterogeneity will support higher biodiversity, providing access to a greater diversity of resources for feeding, breeding, dispersion and overwintering (Benton *et al.*, 2003). The higher heterogeneity also benefits biodiversity due to 'landscape complementation' when access to multiple habitats required for some species to complete their life cycle is facilitated (Dunning *et al.*, 1992; Flick *et al.*, 2012). Similarly, landscapes with higher configurational heterogeneity should support higher biodiversity as complex patterning of the landscape increases the probability that different required resources will be found in close proximity to each other, allowing more efficient access (Dunning *et al.*, 1992; Flick *et al.*, 2012). Although it is acknowledged that landscape heterogeneity may play an important role in explaining biodiversity in these agricultural landscapes, few studies have investigated the effects of surrounding landscape context when assessing the effects of replacing conventional crops with bioenergy crops (Werling *et al.*, 2011).

Our first objective was therefore to test the hypothesis that replacing conventional crops with bioenergy crops will have overall positive effects on biodiversity, recognizing that different taxonomic groups may respond in different ways. This was achieved by quantifying the

species richness, abundance and diversity of five taxonomic groups, representing a range of trophic levels and providers of key ecosystem services (vascular plants, bees (Apidae), hoverflies (Syrphidae) and carabid beetles (Carabidae)) in bioenergy crops, *Miscanthus × giganteus* and oilseed rape (*Brassica napus*). For comparison, we surveyed crops that *Miscanthus* and oilseed rape are likely to replace in Ireland's agricultural landscapes, which are currently dominated by perennial grasslands and to a lesser extent by annual tillage crops. Our second objective was to test the hypothesis that increased compositional and configurational heterogeneity in the surrounding landscapes will result in higher biodiversity in the crop fields. In doing so, we wished to show that the effects of replacing conventional agricultural crops with bioenergy crops, therefore, also depended on surrounding landscape context.

Materials and methods

Study region and study sites

This study was conducted in agriculturally dominated landscapes in south-east Ireland, where tillage crops are interspersed with grassland-based beef and dairy farming. Typical of Irish rural landscapes, most fields were relatively small (mean of 2.8 ha) and surrounded by hedgerows. Fifty fields were selected comprising 10 replicates of five crop types geographically interspersed throughout the study area (Fig. 1). These crop types were oilseed rape (OS); *Miscanthus* planted on former tillage (MT); *Miscanthus* planted on former grassland (MG); winter wheat (control tillage) (CT); and grasslands (control grassland) (CG).

Large-scale commercial planting of *Miscanthus* only started in Ireland in 2006, and so, all *Miscanthus* fields used in the study were 2–3 years old and reaching maturity (Karp & Shield, 2008). Prior to field ploughing and *Miscanthus* rhizome planting, herbicides were sprayed to control perennial weeds. Chemical fertilizer was applied during the establishment phase of *Miscanthus* and depended on the nutrient content of the soil at the specific site (application rates ranging from 30–100, 0–23, 0–120 kg ha⁻¹ for nitrogen, phosphorous and potassium respectively). No fertilizer, pesticide or herbicide inputs were made to the *Miscanthus* crops in subsequent years. Annual chemical fertilizer application rates for the winter wheat and oilseed rape crops ranged from approximately 60–225, 0–45, 0–140 kg ha⁻¹ for nitrogen, phosphorous and potassium respectively. The grassland sites were dominated by perennial ryegrass (*Lolium perenne* L.) and typically managed intensively for silage production. This included annual chemical fertilizer application rates of approximately 225 kg ha⁻¹ for nitrogen, and ranging from 0 to 30 and 0 to 120 kg ha⁻¹ for phosphorous and potassium respectively. Chemical fertilizer application rates varied depending on whether the sites were grazed, the use of organic fertilizers and the nutrient content of the soil at the specific site.

All study fields were at least 1 km apart to minimize potential species overlap between the sites. Fields were also chosen to minimize within crop type variation where possible, with similar sizes, number of hedgerows and altitude, with one field selected per farm to ensure independence of farm management activities.

Species surveys

Five taxonomic groups were surveyed and identified to species level in 50 fields on two occasions during the summer of 2009: vascular plants, carabid beetles (Carabidae) (only sampled in 45 of the fields), bees (Apidae) and hoverflies (Syrphidae). Carabid beetles and plants were surveyed at the margin (non-cropped area beside the hedgerow), edge (5 m from the edge of crop into the field) and centre (20 m into the field from the edge of crop) of the fields, and bees and hoverflies were surveyed in the margin and centre of fields only. Plant diversity and abundance were surveyed by visually recording percentage cover of each species in three 1 × 1 m quadrats, 10 m apart at the margin, edge and centre of each field (nine quadrats in total per site). Plant species nomenclature follows Stace (2010). Carabid beetles were sampled using three pitfall traps, one in each of the margin, edge and centre of fields. Traps were operational for a period of 14 days on two occasions. The rims of the pitfall traps (translucent HDPE lightweight containers, cup size – height 13 cm, top inside diameter 11 cm) were sunk below the soil surface (Luff, 1996) and traps were filled with approximately 100 ml of 1 : 3 parts ethylene glycol and water solution as a killing agent and preservative (Schmidt *et al.*, 2006). A plastic lid placed approximately 2 cm above each trap kept out the rain and debris, and reduced evaporation (Noordijk *et al.*, 2008). The samples were fixed in the laboratory with 70% ethanol. Carabid beetle content of all samples were identified to species according to Luff (2007). Bees and hoverflies were sampled using pan traps (Westphal *et al.*, 2008). Traps comprised three bowls (one painted with blue, one white and one yellow UV paint, Lebuhn & Droege, 2003), set in a metal clamp and adjusted to the height of the surrounding vegetation (Stanley & Stout, 2013). Three traps were placed in the margins of fields, and three in the field centre (20 m apart) for 48 h.

Quantifying landscape context

The landscape composition and configuration surrounding each of the 50 fields were characterized in a 1 × 1 km square with the sampling field at the centre (Fig. S1). Land-use patches that partially overlapped with the square were also mapped in their entirety for the landscape configuration analyses. Digital georeferenced aerial photos were used to spatially map all patches and features in the landscapes. This was followed by field-based surveys identifying land-cover types and habitats in each landscape, combining farmer interviews to determine farm management during the species surveys with ground-truthing of habitats classified according to the national habitat classification system in Ireland (Fossitt, 2000) (Fig. S1). The principal land-use/habitat types included tillage crops, improved agricultural grassland, buildings and artificial

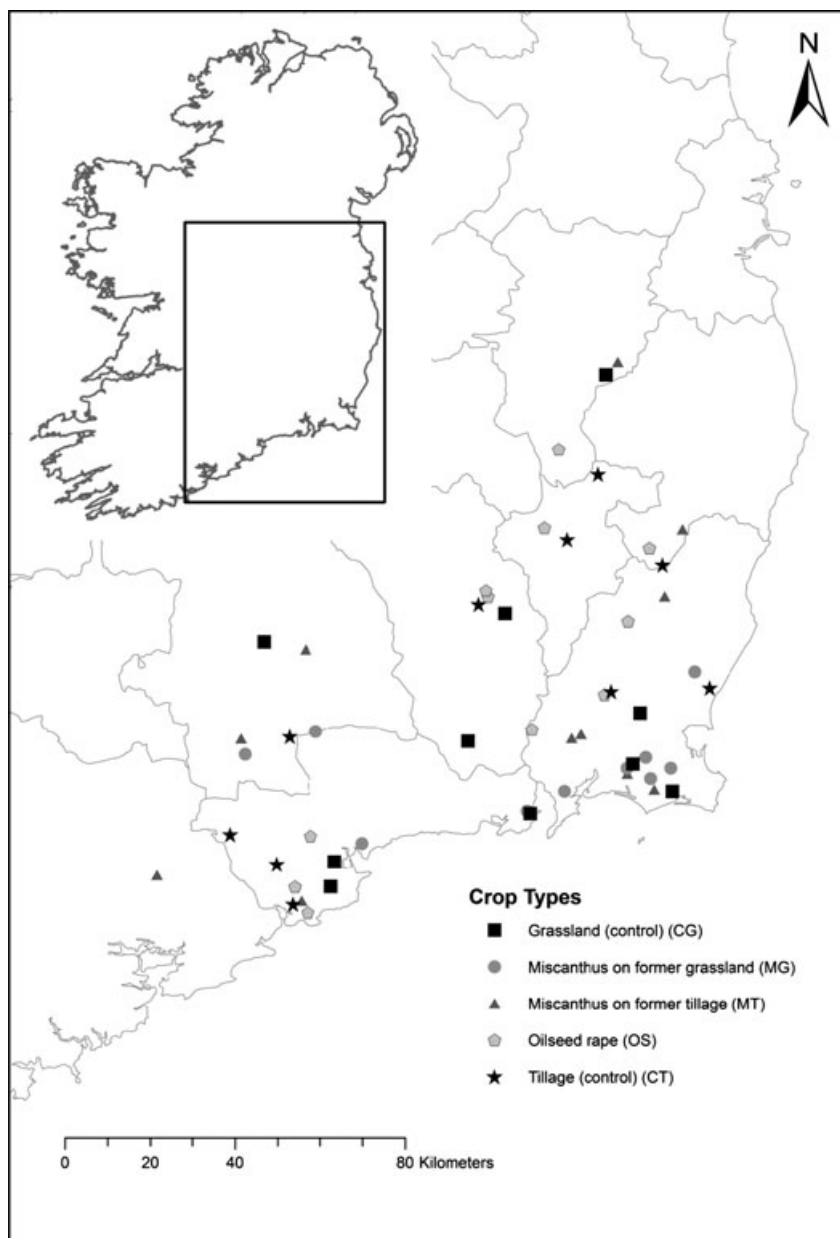


Fig. 1 Map of study region in south-east Ireland including the locations of the 50 fields and landscapes surveyed. These fields represent 10 replicates of five different crop types [oilseed rape (OS), *Miscanthus* planted on former tillage (MT), *Miscanthus* planted on former grassland (MG), tillage (winter wheat) (CT) and grassland (CG)]. Inset shows the location of the study region on the island of Ireland.

surfaces, non-native (highly modified) woodlands, seminatural wet grasslands and seminatural woodlands. Hedgerows were the dominant seminatural linear feature in these landscapes and so, their lengths were also measured. A range of metrics were used to quantify the structure including area, patch density and size, shape and diversity metrics (descriptions in Table S1 in the supplementary material). Calculation of these metrics was based on patches in the landscapes aggregated at the level of individual land-use/habitats (i.e. classes) or at the landscape level (i.e. aggregated classes). All landscape mapping was carried out in ArcGIS v9.3 (ESRI, 2008). Landscape

composition and configuration analyses were carried out using the spatial analysis tools in ArcGIS v9.3 and the ArcGIS extensions Hawth's Tools (Beyer, 2004) and Patch Analyst v4.3 (Rempel *et al.*, 2012).

Data analysis

Species data sampled at the margin, edge and centre of each field were pooled to explore the crop type and landscape context effects.

A range of landscape composition and configuration metrics were considered for analysis. To overcome collinearity between these variables, and to help decrease model complexity, correlations and variance inflation factors (VIF) were used to reduce the number of variables included in the analyses. Variable combinations with VIF values under 5 (Zuur *et al.*, 2007) informed the final selection of variables used in the models, which included: proportion of seminatural habitat, proportion of grassland (strong negative correlation with percentage tillage), hedgerow length, Shannon habitat diversity index, area weighted mean shape index (AWMSI), mean patch fractal dimension index (MPFDI) and edge density (see Table S1 in the supplementary material for further details).

We used poisson generalized linear models (GLMs) to assess the effects of crop type, and habitat context variables on our biodiversity response variables [species richness, species abundance and Chao's species diversity estimator – which accounts for rare species (Chao, 1984)]. These models used as the response variables (species richness and abundance) were based on count data or derived from count data. Overdispersion was accounted for by allowing for extra variation with quasi-GLMs. Initially, we used approximate *F*-tests (Zuur *et al.*, 2009) to specifically assess the effects of crop type (i.e. compare bioenergy crops with conventional crops), for each response. This was followed by an information-theoretic (IT) approach to assess the combined effects of local (crop type) and landscape variables on the response variables. The advantage of this was to avoid selecting a single best model for each response, using the IT approach to find a 95% confidence set of models based on comparing the fits of a predetermined suite of candidate models with Akaike's Information Criterion (AIC), corrected for overdispersion and small sample [QAICc = $(-2LL/c-hat)+2k(k+1)/(n-k-1)$ – where LL is loglikelihood, *c-hat* is dispersion parameter, *k* is number of parameters in the model and *n* is the effective sample size, taken to be number of sites in this article] (Burnham & Anderson, 2002; Whittingham *et al.*, 2006). We ran two sets of models: one exploring the influence of landscape composition (four variables); the other exploring the influence of landscape configuration (three variables). These were considered separate analyses because of limits in number of sites (a full model with all variables would be estimating 14 parameters). Based on differences in QAICc, each model was assigned an Akaike weight (w_i), which for the full set of possible models sum to 1, therefore giving w_i a probabilistic interpretation in terms of the probability of each model being selected as the best-fitting model. The 95% confidence set of models corresponds to the set of models for which the cumulative w_i sum

to 0.95 and contains with 95% certainty the model that best describes the true model, given the collected data.

From this 95% set of models, we then calculated Akaike weighted average parameter values for each explanatory variable. For example, model-averaged parameter β_j was calculated as:

$$\bar{\beta}_j = \sum_{i=1}^n w_i \hat{\beta}_{j,i}$$

where w_i is the Akaike weight of model *i*, and β_j is the estimate of β_j if predictor *j* is included in model *i* or is zero otherwise. We calculated relative variable importance for each predictor by summing the w_i of each model the variable was included in the 95% set of models and dividing by 0.95. This gave a comparative importance index for each variable (including those not appearing in the best model), relative to crop type, which was kept in all models (relative importance for crop type was therefore 1). These 'variable weights' approximate the likelihood that the *i*th variable will appear in the best model in repeated runs of an experiment. They quantify support for a variable across the entire model set and allow the relative importance of all variables (including those not appearing in the best model) to be compared. All statistics were performed using R (R Development Core Team, 2008).

Results

Species richness and abundance

In total, 239 solitary bee, 852 bumblebee and 1519 hoverfly individuals were collected in the pan traps, comprising 23 solitary bee, 8 bumblebee and 43 hoverfly species (Table 1; see Table S2 for complete species lists). Low numbers of honeybees (*Apis mellifera*, 73 individuals) were found and excluded from further analyses. Bumblebees were dominated by the *Bombus sensu stricto* group (comprising *Bombus terrestris*, *B. lucorum* and *B. cryptarum*, see Stanley *et al.*, 2013) (40%), followed by *B. hortorum* (26%). Hoverflies were dominated by *Helophilus pendulus* (46%) and *Eristalis arbustorum* (13%). Solitary bees were dominated by *Andrena angustior*, *Andrena bicolor* and *Andrena fucata* (18, 17 and 11% respectively), followed by *Halictus rubicundus* (10%). A total of 8264 individuals from 51 carabid beetle species

Table 1 Total and mean species richness, abundance and diversity (\pm standard error) of the five taxonomic groups for all sites

Taxonomic group	Total species richness	Total abundance	Mean species richness/site	Mean abundance/site	Mean diversity (Chao)/site	Proportion of national fauna/flora (%)
Carabid beetles	51	8264	15.6 (\pm 4.4)	183.6 (\pm 179.4)	19.7 (\pm 7.7)	24
Bumblebees	8	852	3.9 (\pm 1.4)	16.8 (\pm 14.7)	4.5 (\pm 2.0)	23
Solitary bees	23	239	2.5 (\pm 1.9)	4.8 (\pm 4.8)	3.6 (\pm 4.0)	40
Hoverflies	43	1519	7.0 (\pm 3.4)	30.2 (\pm 24.8)	11.3 (\pm 10.6)	28
Vascular plants	124	NA	25.5 (\pm 7.3)	5.9 (\pm 4/6)	NA	10

were collected in the pitfall traps, dominated by *Anchomenus dorsalis* (21%), *Pterostichus melanarius* (17%), *Nebria brevicollis* (13%) and *Pterostichus madidus* (8%). In addition, 125 vascular plant species were identified in the quadrats, dominated by a mix of grasses including *Holcus lanatus*, *Arrhenatherum elatius*, *Lolium perenne* and *Poa annua*, and forbs including *Ranunculus repens*, *Urtica dioica*, *Galium aparine* and *Epilobium spp.* Dominant woody hedgerow species recorded included *Rubus fruticosus* agg., *Hedera helix*, *Ulex europaeus*, *Prunus spinosa* and *Crataegus monogyna*.

Crop type effects

An overall significant crop type effect was found for all response variables representing species richness, abundance and diversity of the five taxonomic groups (Table 2). Solitary bee richness, abundance and diversity were significantly higher in OS than CG and CT (Fig. 2), whereas solitary bee richness was significantly higher in MT than in CG (Fig. 2a). No significant differences in solitary bee abundance and diversity were found between the three perennial crops CG, MT and MG (Fig. 2). Plant richness was significantly lower in CT than all other crops types, with no differences found

Table 2 *F*-values and levels of significance from generalized linear models testing the effects of crop type (tillage, oilseed rape, *Miscanthus* on former tillage, grassland, *Miscanthus* on former grassland) on species richness, abundance and diversity. Number of fields per crop type = 10

Response Variable	<i>F</i> -value
Hoverflies	
Richness	100.868***
Abundance	74.352***
Diversity (Chao Index)	51.684***
Bumblebees	
Richness	96.752***
Abundance	62.741***
Diversity (Chao Index)	75.155***
Solitary bees	
Richness	12.524***
Abundance	15.483***
Diversity (Chao Index)	14.700***
Vascular plants	
Richness	1083.444***
Carabid beetles	
Richness	594.165***
Abundance	88.650***
Diversity (Chao Index)	241.929***

**P* < 0.05.

***P* < 0.01.

****P* < 0.001.

between the other four crop types (Fig. 2a). No significant differences in carabid beetle diversity were found between crop types (Fig. 2c). However, carabid beetle richness and abundance were significantly higher in the two annual crops (OS and CT) compared with the three perennial crops (CG, MG, MT), with no significant differences found between either the annual or perennial crops (Fig. 2a and b). No significant pairwise differences in hoverfly and bumblebee richness, abundance or diversity were found between crop types (Fig. 2).

Landscape context

The 50 landscapes were dominated by agricultural improved grassland and tillage cropping systems, with mean proportions of 45% and 41%, of the total landscape respectively. SeminatURAL habitats accounted for just under 3% (range 0–16%) of the landscapes, and included seminatural wet grassland (1.4%), freshwater marsh (0.46%), scrub (0.89%), oak–ash–hazel woodland (0.10%), riparian woodland (0.01%) and wet willow–alder–ash woodland (0.08%). A mean of 10.37 km of hedgerows was found per landscape, ranging from 3 to 18 km. Overall, the compositional heterogeneity of the landscapes was represented by Shannon's habitat diversity index, which ranged from 0.2523 to 1.648 with a mean value of 0.9871. Mean patch size was approximately 2.7 hectares, whereas on average, each landscape had 67 patches. The AWMSI and MPFDI were 1.322 and 1.343 (1 = perfectly simple shape (circle or square); >1 = more shape complexity), respectively, whereas edge density was just over 258 m ha⁻¹. More details on the landscape metrics can be found in Table S1 in the supplementary material.

Landscape composition and configuration effects

No significant relationships were found between plant richness and any of the landscape composition and configuration variables, with crop type the only explanatory variable significantly explaining the variation (Table 3), with minimal support from variable weights (summed w_i ranged from 0.17 to 0.44). Bumblebees were also found mostly not to be responding to the landscape composition and configuration variables, except for one very strong negative association between abundance and the proportion of grassland in the landscapes (Table 3; Fig. 3e), supported by variable weights (summed $w_i = 0.70$). Solitary bee richness and abundance were found to have positive associations with MPFDI (Table 3; Fig. 4f), and solitary bee abundance was also positively associated with habitat diversity (Table 3; Fig. 3f). In addition, solitary bee diversity was negatively associated with seminatural habitat cover

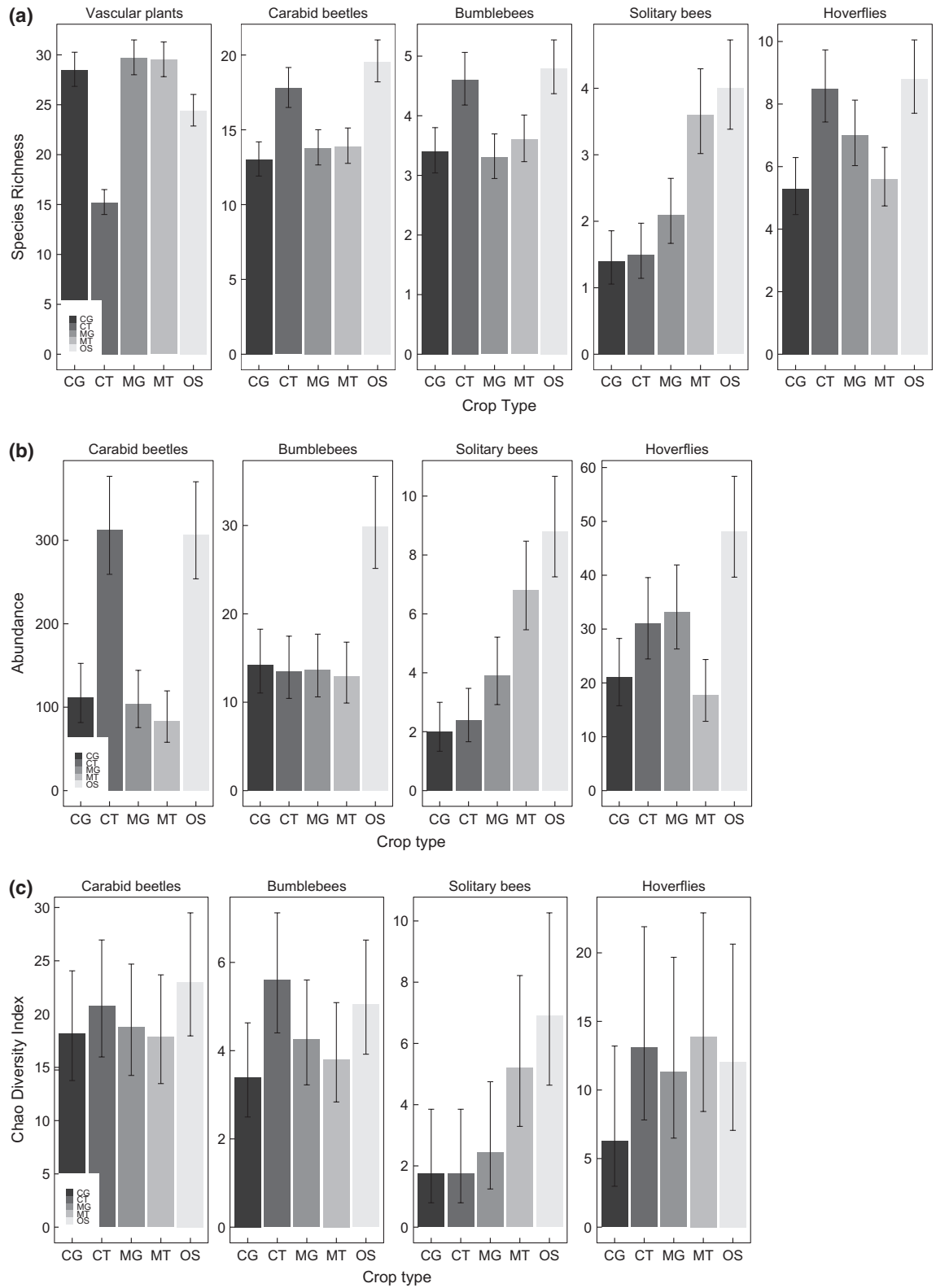


Fig. 2 Mean (\pm SE) species richness (a), abundance (b) and diversity (Chao's Index) (c) of the five taxonomic groups found in the five crop types (grassland (CG), tillage (CT), *Miscanthus* on former grassland (MG), *Miscanthus* on former tillage (MT), oilseed rape (OS)). Results are from generalized linear models (see Table 2).

Table 3 Parameter estimates from information-theoretic models (model averaging) for the species richness, abundance and diversity of the five taxonomic groups and landscape context. Crop type was included in all models

Response variable	Landscape composition			Landscape configuration			Edge Density
	Hedgerow length	% SeminatURAL habitats	% Grassland	Shannon Habitat Diversity Index	Area Weighted Mean Shape Index	Mean Patch Fractal Dimension Index	
Hoverflies							
Richness	0.083562	0.002107	0.167931*	0.078381	-0.05827	-0.05515	0.184
Abundance	0.17318***	-0.04802	0.07519	0.0653	-0.16894***	-0.07134	0.18589***
Diversity (Chao Index)	0.04979	0.19473**	0.31286***	0.2883***	0.07393	-0.07654	0.42186***
Bumblebees							
Richness	0.04751	-0.01656	-0.08617	0.09557	-0.04486	0.01789	0.09239
Abundance	0.038801	-0.07235	-0.27399***	0.000173	0.05397	-0.06601	-0.0415
Diversity (Chao Index)	0.008593	-0.0671	-0.08079	0.18252	-0.02179	0.05262	0.11186
Solitary bees							
Richness	-0.02598	-0.11334	0.07237	0.03059	-0.12378	0.17046**	0.01018
Abundance	-0.07746	-0.12829	-0.15895	0.21571*	-0.07367	0.28645	-0.14615
Diversity (Chao Index)	-0.06359	-0.19912*	0.09358	-0.04427	-0.17027	0.25646*	-0.07042
Vascular plants							
Richness	0.04827	-0.03033	0.0419	-0.02922	-0.02462	0.03481	-0.01795
Carabid beetles							
Richness	-0.06876	-0.10804*	-0.07333	-0.04938	-0.00753	-0.04519	-0.16053*
Abundance	-0.1931***	-0.3845***	-0.14659***	-0.10315	-0.49921***	0.14522***	-0.04762***
Diversity (Chao Index)	-0.09228*	-0.13034*	-0.06705	-0.14232**	-0.0445	-0.08158	-0.28149***

Parameter estimates of additional variables included in the model are presented below with significant results highlighted in bold: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. The parameter estimates presented below are the averages across 95% models (weighted by selection probabilities); the models represent 95% confidence for the data set. Models were run separately for the landscape composition and configuration data sets. Full details of the 95% confidence set of all landscape configuration and composition models for each response variable can be found in Tables S3–S28 in the supplementary material.

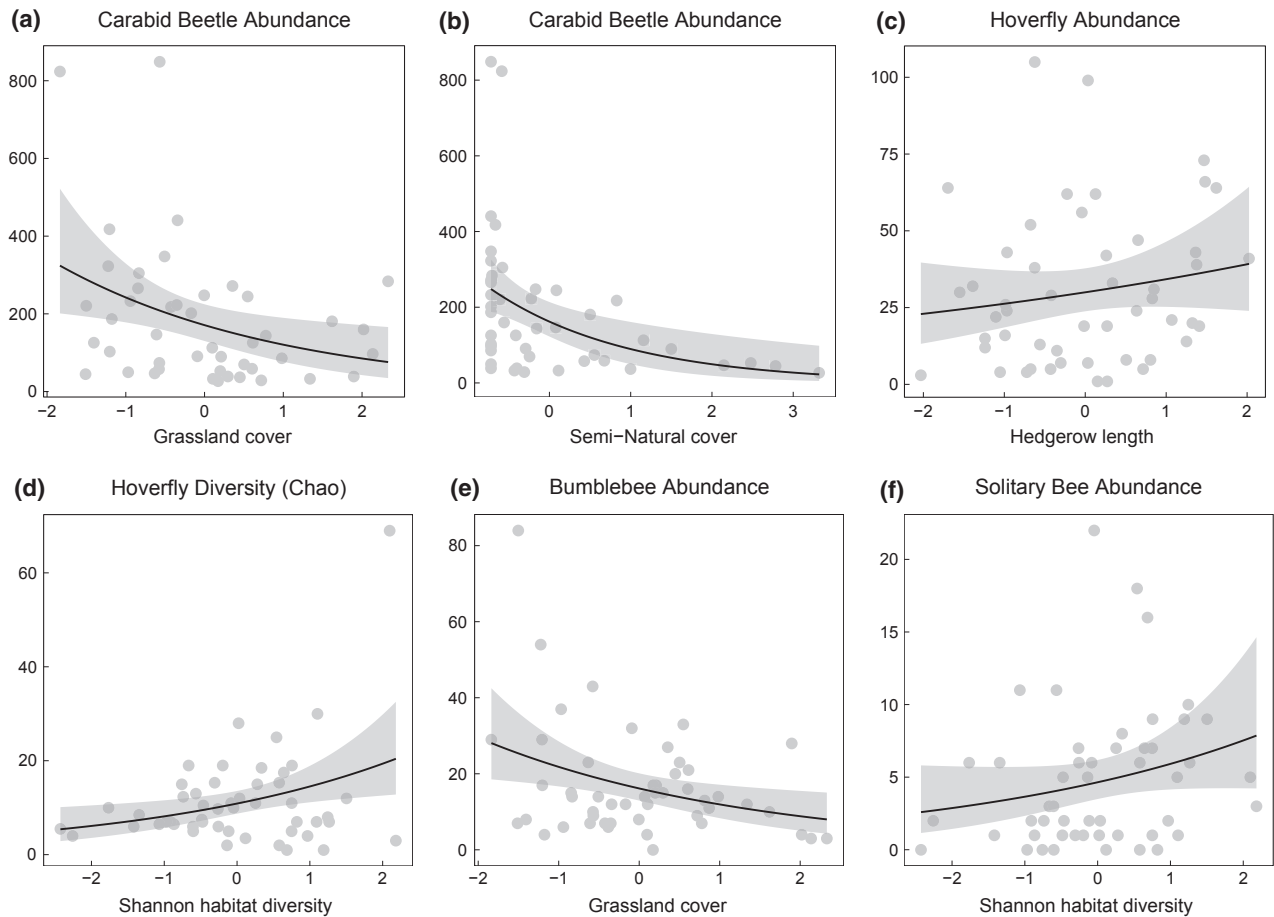


Fig. 3 Selected relationships between species response variables and landscape composition: (a) carabid beetle abundance and % grassland, (b) carabid beetle abundance and percentage seminatural habitat, (c) hoverfly abundance and hedgerow length, (d) hoverfly diversity and Shannon's habitat diversity index, (e) bumblebee abundance and percentage grassland and (f) solitary bee abundance and Shannon's habitat diversity index. Data are aggregated across all crop types as no significant crop type–landscape context interactions were found. All explanatory variables are standardized. Shaded bands represent 95% confidence intervals.

(Table 3). Overall, carabid beetles and hoverflies were the most responsive taxonomic groups to landscape composition and configuration (Table 3; Figs. 3 and 4). The importance of landscape context variables in explaining the variation relative to crop type was highest for these two groups, particularly in terms of the proportion of the landscapes occupied by seminatural habitats and landscapes with higher edge density, supported by high variable weights. Carabid beetle abundance, in particular, was negatively associated with hedgerow length, the proportion of seminatural habitats and percentage grassland (Table 3; Fig. 3a and b), AWMSI and edge density (Table 3), while being positively associated with MPDFI (Table 3). Carabid beetle diversity was similarly negatively associated with hedgerow length, percentage seminatural habitats, Shannon habitat diversity index and edge density (Table 3; Fig. 4b), whereas carabid beetle richness was negatively associated with percentage seminatural habitats and

edge density (Table 3). Conversely, hoverflies were positively associated with all the landscape composition variables (Table 3; Figs 3c and d), and edge density (Table 3; Figs 4c and d), while being negatively associated with AWMSI (Table 3). Full details of the 95% confidence set of landscape configuration and composition models for each response variable can be found in Tables S3–S28 in the supplementary material.

Crop type and landscape interactions

Although crop type was shown to significantly affect the richness, abundance and diversity of all five taxonomic groups, and landscape context was also independently affecting the richness, abundance and diversity of the hoverflies and carabid beetles, no significant interaction effects between crop type and the landscape context variables were found (mean p values ranged from 0.34 to 0.69).

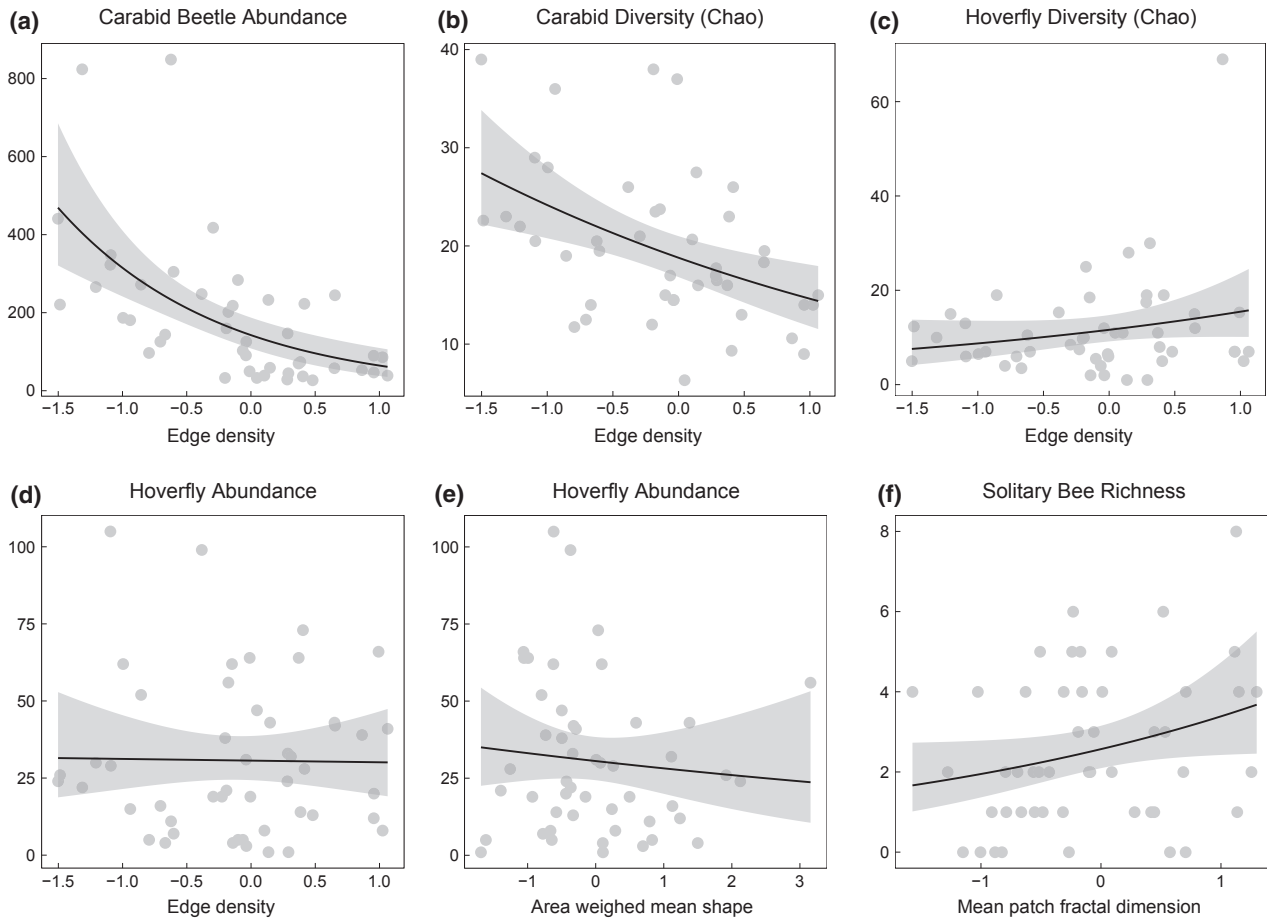


Fig. 4 Selected relationships between species response variables and landscape configuration: (a) carabid beetle abundance and edge density, (b) carabid beetle diversity and edge density, (c) hoverfly diversity and edge density, (d) hoverfly abundance and edge density, (e) hoverfly abundance and AWMSI, and (f) solitary bee richness and MPFDI. Data are aggregated across all crop types as no significant crop type–landscape context interactions were found. All explanatory variables are standardized. Shaded bands represent 95% confidence intervals.

Discussion

The results of our study support the hypothesis that at the local scale, the biodiversity associated with two bioenergy crops, *Miscanthus* and oilseed rape, was comparatively better or no worse than conventional grassland and tillage crops for most of the taxonomic groups studied. We found no significant differences between the two *Miscanthus* crops, which replaced former conventional grassland and tillage crops. The key differences were shown between the perennial and annual crops; importantly, however, the five taxonomic groups did not respond in a consistent way. Of the two bioenergy crops, oilseed rape was comparatively better than the two *Miscanthus* crops for the solitary bees and the carabid beetles, with few differences found in the other taxonomic groups. Our results also supported the hypothesis that surrounding landscape compositional

and configurational heterogeneity played a role in explaining species richness, abundance and diversity in these agricultural landscapes, and that the combined effects of crop type and surrounding landscape context were additive.

Crop type effects

The finding that different taxonomic groups respond in different ways to crop type and the surrounding landscape context is consistent with many other studies (Burel *et al.*, 2004; Batáry *et al.*, 2012). It was hypothesized that perennial *Miscanthus* and conventional grassland crops should generally be more beneficial for biodiversity when compared with oilseed rape and conventional tillage (winter wheat) because of lower inputs and greater within-habitat spatial heterogeneity. However, although other studies have shown greater benefits of

extensively managed or seminatural perennial crops compared with more intensively managed crops (Bianchi *et al.*, 2006; Fargione *et al.*, 2009; Werling *et al.*, 2011), we found that except for some benefits for solitary bee richness, the biodiversity in the *Miscanthus* fields was very similar to that in the conventional grassland fields, and suggest that more time may be needed to see additional benefits to biodiversity in these relatively young 3 year old *Miscanthus* fields.

Vascular plant richness was significantly lower in the conventional tillage (winter wheat) compared with all other crops. This is not surprising as field-scale variables such as boundary type, fertilizer and herbicide application rates, grazing management and soil properties are known to be key drivers of plant richness at this scale (Gabriel *et al.*, 2005; Batáry *et al.*, 2012; Power *et al.*, 2012). Contrary to the proposed hypothesis, we showed that solitary bee and carabid beetle richness and abundance were higher in the oilseed rape compared with the perennial crops. For the carabid beetles, there was also a decrease in abundance when replacing former tillage land with *Miscanthus*. The carabid beetles in this study were sampled during the summer months and we suggest that higher prey densities in the annual crops (e.g. cereal aphids) explain the higher species richness and abundance (Bohan *et al.*, 2000; Anjum-Zubair *et al.*, 2010), whereas the additional floral resources provided by the mass flowering oilseed rape contribute to the effects on bees (Stanley & Stout, 2013).

Landscape composition and configuration effects

We showed that replacing conventional agricultural crops with bioenergy crops is independent of surrounding landscape context because of the lack of interactions between crop type and landscape structure. Importantly, this, therefore, suggests that the responses of the five taxonomic groups to *Miscanthus* and oilseed rape cultivation would hold across a variety of landscape contexts (Werling *et al.*, 2011). However, the importance of surrounding landscape context for some taxonomic groups cannot be ignored as strong independent relationships with landscape composition and configuration were found in our study.

We found negative relationships between solitary bee diversity and increasing seminatural habitat cover. We suggest that this can be explained by the types of seminatural habitats found in these landscapes, mostly dominated by woodlands, wet grassland and freshwater marsh, habitats known not to significantly benefit bees (Steffan-Dewenter *et al.*, 2002). Conversely, we found positive associations for solitary bees with habitat diversity and MPFDI, which highlights the importance of landscape heterogeneity for this taxonomic group

(Banaszak, 1992), particularly at smaller scales as they have shorter foraging ranges than bumblebees (Steffan-Dewenter *et al.*, 2002). The only relationship found between bumblebees and landscape context was a negative association with increasing grassland cover. This is probably because intensive agricultural grasslands contain fewer floral resources compared with other land-use types (Holzschuh *et al.*, 2007; Power & Stout, 2011; Stanley & Stout, 2013). It is likely that we did not find any other relationships between bumblebees and landscape variables because we only considered 1 km² areas. Previous studies have tended to demonstrate landscape effects on bumblebees at larger scales (2–3 km) (Steffan-Dewenter *et al.*, 2002; Westphal *et al.*, 2006; Diaz-Forero *et al.*, 2012). In contrast to most studies, we found no significant relationships between vascular plant richness and surrounding landscape context (Gabriel *et al.*, 2005; Batáry *et al.*, 2012; Power *et al.*, 2012). Similar to the bumblebees, this again suggests that plant richness in more intensively managed agricultural landscapes may be explained at larger landscape scales (Gabriel *et al.*, 2005; Power *et al.*, 2012).

We found stronger positive associations between landscape heterogeneity and hoverfly richness, abundance and diversity compared with the other two pollinating taxa, which support other studies carried out at similar scales (Kleijn & van Langevelde, 2006). Meyer *et al.* (2009) also found that hoverfly species richness increased with increasing landscape diversity at a 250 m radius, and suggested that diverse landscapes provide a diverse range of micro- and macrohabitats for adults and larvae. However, they also showed that hoverfly density decreased with increasing landscape diversity at a 750 m radius, and proposed that this was because abundance was dependent on the quantity of resources available, such as the amount of pollen and nectar resources for adults and the amount of larval macrohabitats in the surrounding matrix.

In contrast to the hoverflies, most landscape heterogeneity variables (hedgerow length, percentage seminatural habitats, percentage grassland and edge density) were negatively associated with carabid beetle richness, abundance and diversity. This is in contrast to many studies that showed higher landscape heterogeneity supporting higher carabid beetle richness in tillage crops (Dauber *et al.*, 2005; Batáry *et al.*, 2007), whereas for perennial crops, other studies have shown that higher surrounding landscape heterogeneity may provide alternative and perhaps higher quality habitats, thereby reducing the potential carabid beetle richness and abundance in these fields (Wamser *et al.*, 2011). However, in our study, the response of the carabid beetles to landscape structure was constant across all crop types. The composition of the surrounding

landscape, in particular the amount of non-crop habitats such as hedgerows, field margins and seminatural habitats, is known to provide important resources to carabid beetles (e.g. overwintering habitat) (Coombes & Sotherton, 1986; Andersen, 1997; Bianchi *et al.*, 2006; Billeter *et al.*, 2008). Our data showed that it was those landscapes with higher proportions of annual crops that had less compositional and configurational heterogeneity accounting for the negative landscape associations.

Importance of landscape heterogeneity and landscape-scale assessments

The variety in responses of the five taxonomic groups reflects the different nesting, overwintering and foraging resource requirements, different life history traits and mobility/dispersal patterns, and which landscape variables they are sensitive (Burel *et al.*, 2004). The different relationships among the five taxonomic groups, crop type and the surrounding landscape context, therefore, confirms the overall need for maintaining or increasing heterogeneity in agricultural landscapes, not only through the maintenance of cropping system mosaics and the presence of seminatural habitats and features but also to maintain or increase the less well-studied configurational heterogeneity within the productive crops (Fahrig *et al.*, 2011; Flick *et al.*, 2012).

Overall, we can conclude that the cultivation of bioenergy crops in Ireland, in general, had positive effects on the species richness of a wide range of taxa when compared with conventional crops (Dauber *et al.*, 2010), and that while landscape heterogeneity overall is very important for biodiversity, field-scale effects were independent of surrounding landscape context. This indicates that maximizing the abundance and diversity of species, associated ecosystem functions and the delivery of ecosystem services will be best achieved by maintaining landscape compositional (including diverse mosaics of both food and bioenergy crops) and configurational heterogeneity.

It must be remembered that the results in this study reflect low-density planting of bioenergy crops in Ireland to date, and thus large-scale replacement of conventional crops with novel bioenergy crops and changes to the current land-use mosaics in Ireland's landscapes are increasingly likely as schemes in Ireland and Europe target significantly more planting in the coming years. So, although we can say that the introduction of *Miscanthus* and oilseed rape into agricultural landscapes did not result in an obvious negative impact on biodiversity measured at the field scale, EU renewable energy policies are driving an increase in the planting of bioenergy crops, and it is likely that the effects of large-scale

planting in these landscapes could result in very different impacts on the biodiversity with consequences for ecosystem functioning.

Therefore, we can also conclude that greater knowledge of spatial processes across ecosystems, and not just what we measure at the field scale, is critical to better understand the effects of landscape changes on biodiversity and ecosystem functioning and services (Christian *et al.*, 1998; Tschardtke *et al.*, 2005). This means that for an impact assessment, the mainly positive or neutral effects on biodiversity that we report at the field scale here, would require additional landscape-scale assessments to fully take landscape-scale ecological processes into account (Dauber *et al.*, 2010). A greater understanding of aggregated impacts (ecological, socio-economic) at the landscape scale can contribute to improved impact assessment and planning, helping achieve win-win solutions for biodiversity conservation and bioenergy production and the sustainable development of climate change mitigation measures (Fargione *et al.*, 2009; Dauber *et al.*, 2012).

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Supporting Information

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

Figure S1: Four landscapes illustrating a range of landscape compositions (a) high Shannon Habitat Diversity (1.370), and (b) low Shannon Habitat Diversity (0.252), and configuration structures (c) low Area Weighted Mean Shape Index (1.209) and (d) high Area Weighted Mean Shape Index (1.533). Legend: BC1 = Tillage crops; BC2 = Horticultural land; BL3 = Buildings and artificial surfaces; GA1 = Improved agricultural grassland; GS4 = Wet grassland (seminatural); WN5 = Riparian woodland; WN6 = Wet willow–alder–ash woodland; WD1 = (Mixed) broadleaved woodland; WD2 = Mixed broadleaved/conifer woodland; WD4 = Conifer plantation; WS1 = Scrub; WS2 = Immature woodland; ED4 = Active quarries and mines; GSI = semi-improved grassland; AES = agri-environment measure for biodiversity; FS1 = Reed and large sedge swamps (habitats classified according to Fossitt (2000)).

Table S1: Summary statistics and descriptions of landscape composition and configuration metrics used in this study. Variables marked with asterisks were retained in the analyses presented in Table 3 and Figures 3 and 4 after testing for collinearity with correlation and variance inflation factors.

Table S2: Complete species lists for the five taxonomic groups surveyed in this study.

Table S3a: Carabid beetle species richness 95% set of landscape configuration models. First column corresponds to terms included in each model and these are defined in Table S3b.

Table S3b: Carabid beetle species richness relative variable importance and term codes.

Table S4a: Carabid beetle abundance 95% set of landscape configuration models. First column corresponds to terms included in each model and these are defined in Table S4b.

Table S4b: Carabid beetle abundance relative variable importance and term codes.

Table S5a: Carabid beetle diversity (Chao’s Index) 95% set of landscape configuration models. First column corresponds to terms included in each model and these are defined in Table S5b.

Table S5b: Carabid beetle diversity (Chao’s Index) relative variable importance and term codes.

Table S6a: Plant species richness 95% set of landscape configuration models. First column corresponds to terms included in each model and these are defined in Table S6b.

Table S6b: Plant species richness relative variable importance and term codes.

Table S7a: Solitary bee species richness 95% set of landscape configuration models. First column corresponds to terms included in each model and these are defined in Table S7b.

Table S7b: Solitary bee species richness relative variable importance and term codes.

Table S8a: Solitary bee abundance 95% set of landscape configuration models. First column corresponds to terms included in each model and these are defined in Table S8b.

Table S8b: Solitary bee abundance relative variable importance and term codes.

Table S9a: Solitary bee diversity (Chao's Index) 95% set of landscape configuration models. First column corresponds to terms included in each model and these are defined in Table S9b.

Table S9b: Solitary bee diversity (Chao's Index) relative variable importance and term codes.

Table S10a: Bumblebee species richness 95% set of landscape configuration models. First column corresponds to terms included in each model and these are defined in Table S10b.

Table S10b: Bumblebee species richness relative variable importance and term codes.

Table S11a: Bumblebee abundance 95% set of landscape configuration models. First column corresponds to terms included in each model and these are defined in Table S11b.

Table S11b: Bumblebee abundance relative variable importance and term codes.

Table S12a: Bumblebee diversity (Chao's Index) 95% set of landscape configuration models. First column corresponds to terms included in each model and these are defined in Table S12b.

Table S12b: Bumblebee diversity (Chao's Index) relative variable importance and term codes.

Table S13a: Hoverfly species richness 95% set of landscape configuration models. First column corresponds to terms included in each model and these are defined in Table S13b.

Table S13b: Hoverfly species richness relative variable importance and term codes.

Table S14a: Hoverfly abundance 95% set of landscape configuration models. First column corresponds to terms included in each model and these are defined in Table S14b.

Table S14b: Hoverfly abundance relative variable importance and term codes.

Table S15a: Hoverfly diversity (Chao's Index) 95% set of landscape configuration models. First column corresponds to terms included in each model and these are defined in Table S15b.

Table S15b: Hoverfly diversity (Chao's Index) relative variable importance and term codes.

Table S16a: Carabid beetle species richness 95% set of landscape composition models. First column corresponds to terms included in each model and these are defined in Table S16b.

Table S16b: Carabid beetle species richness relative variable importance and term codes.

Table S17a: Carabid beetle abundance 95% set of landscape composition models. First column corresponds to terms included in each model and these are defined in Table S17b.

Table S17b: Carabid beetle abundance relative variable importance and term codes.

Table S18a: Carabid beetle diversity (Chao's Index) 95% set of landscape composition models. First column corresponds to terms included in each model and these are defined in Table S18b.

Table S18b: Carabid beetle diversity (Chao's Index) relative variable importance and term codes.

Table S19a: Plant species richness 95% set of landscape composition models. First column corresponds to terms included in each model and these are defined in Table S19b.

Table S19b: Plant species richness relative variable importance and term codes.

Table S20a: Solitary bee species richness 95% set of landscape composition models. First column corresponds to terms included in each model and these are defined in Table S20b.

Table S20b: Solitary bee species richness relative variable importance and term codes.

Table S21a: Solitary bee abundance 95% set of landscape composition models. First column corresponds to terms included in each model and these are defined in Table S21b.

Table S21b: Solitary bee abundance relative variable importance and term codes.

Table S22a: Solitary bee diversity (Chao's Index) 95% set of landscape composition models. First column corresponds to terms included in each model and these are defined in Table S22b.

Table S22b: Solitary bee diversity (Chao's Index) relative variable importance and term codes.

Table S23a: Bumblebee species richness 95% set of landscape composition models. First column corresponds to terms included in each model and these are defined in Table S23b.

Table S23b: Bumblebee species richness relative variable importance and term codes.

Table S24a: Bumblebee abundance 95% set of landscape composition models. First column corresponds to terms included in each model and these are defined in Table S24b.

Table S24b: Bumblebee abundance relative variable importance and term codes.

Table S25a: Bumblebee diversity (Chao's Index) 95% set of landscape composition models. First column corresponds to terms included in each model and these are defined in Table S25b.

Table S25b: Bumblebee diversity (Chao's Index) relative variable importance and term codes.

Table S26a: Hoverfly species richness 95% set of landscape composition models. First column corresponds to terms included in each model and these are defined in Table S26b.

Table S26b: Hoverfly species richness relative variable importance and term codes.

Table S27a: Hoverfly abundance 95% set of landscape composition models. First column corresponds to terms included in each model and these are defined in Table S27b.

Table S27b: Hoverfly abundance relative variable importance and term codes.

Table S28a: Hoverfly diversity (Chao's Index) 95% set of landscape composition models. First column corresponds to terms included in each model and these are defined in Table S28b.

Table S28b: Hoverfly diversity (Chao's Index) relative variable importance and term codes.