Yield-biodiversity trade-off in patchy fields of *Miscanthus × giganteus*

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Abstract

Increasing crop productivity to meet rising demands for food and energy, but doing so in an environmentally sustainable manner, is one of the greatest challenges for agriculture to date. In Ireland, *Miscanthus × giganteus* has the potential to become a major feedstock for bioenergy production, but the economic feasibility of its cultivation depends on high yields. Miscanthus fields can have a large number of gaps in crop cover, adversely impacting yield and hence economic viability. Predominantly positive effects of Miscanthus on biodiversity reported from previous research might be attributable to high crop patchiness, particularly during the establishment phase. The aim of this research was to assess crop patchiness on a field scale and to analyse the relationship between Miscanthus yield and species richness and abundance of selected taxa of farmland wildlife. For 14 Miscanthus fields at the end of their establishment phase (4–5 years after planting), which had been planted either on improved grassland (MG) or tilled arable land (MT), we determined patchiness of the crop cover, percentage light penetration (LP) to the lower canopy, Miscanthus shoot density and height, vascular plants and epigeic arthropods. Plant species richness and noncrop vegetation cover in Miscanthus fields increased with increasing patchiness, due to higher levels of LP to the lower canopy. The species richness of ground beetles and the activity density of spiders followed the increase in vegetation cover. Plant species richness and activity density of spiders on both MT and MG fields, as well as vegetation cover and activity density of ground beetles on MG fields, were negatively associated with Miscanthus yield. In conclusion, positive effects of Miscanthus on biodiversity can diminish with increasing productivity. This matter needs to be considered when assessing the relative ecological impacts of developing biomass crops in comparison with other land use.

Keywords: Araneae, Carabidae, crop cover, light penetration, Miscanthus establishment, patchiness, vascular plants, vegetation cover

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Introduction

With global biodiversity and economic crises, the influence and interaction between productivity and conservation becomes increasingly important. The agricultural practices adopted to achieve high crop yields are recognized as strong drivers of biodiversity loss (Foley *et al.*, 2005; Geiger *et al.*, 2010). A principle strategy to feed and fuel a growing human population is to further increase crop yields, but there is concern that doing so in an environmentally sustainable manner might stretch trade-offs between production and biodiversity conservation beyond limits (Cunningham *et al.*, 2013). Within the rapidly developing sector of bioenergy crops, there

is both great concern and great expectation with respect to the conservation of farmland biodiversity (Sala *et al.*, 2009; Nuffield Council on Bioethics, 2011; Wiens *et al.*, 2011). To ensure that the potential benefits of bioenergy crops for climate, energy, ecology and economy are fulfilled, it is vital that the environmental and ecological impacts of their production are assessed (Firbank, 2008; Byrne & Stone, 2011).

In agroecosystems, species richness is often correlated with the spatial and functional heterogeneity of the environment (Benton *et al.*, 2003; Fahrig *et al.*, 2011). Establishing new biomass crops will either increase or decrease the heterogeneity of agroecosystems, depending on the type of land use replaced and the scale of their establishment, and thus have either positive or negative consequences for farmland biodiversity (Anderson & Fergusson, 2006; Dauber *et al.*, 2010; Pedroli *et al.*, 2013).

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The low agrochemical inputs required by perennial grass crops such as Miscanthus, as well as the nonannual cycles of soil disturbance, should result in high intrinsic biodiversity value of those crops (Sage, 1998; Anderson & Fergusson, 2006; Haughton et al., 2009; Smeets et al., 2009). Many studies on noncrop vegetation and fauna in perennial biomass crops report benefits to farmland biodiversity due to a high physical heterogeneity of the crops (e.g. Coates & Say, 1999; Bellamy et al., 2009; Gardiner et al., 2010), the temporal stability of the habitats they provide and the relatively low impact methods by which they are managed (Rowe et al., 2009). Our knowledge about the nature and quantity of resources provided to farmland taxa by novel biomass crops such as Miscanthus is, however, still limited (Dauber et al., 2010). Hence, there is some concern when areas considered marginal for agricultural production, containing habitats of high biodiversity value, are discussed as promising localities for bioenergy crop production (Eggers et al., 2009; Dauber et al., 2012; Harvolk et al., 2013).

Several studies reported positive or neutral effects of Miscanthus on species-level biodiversity in comparison with conventional agricultural fields, but effects vary according to the type of conventional crop Miscanthus is compared with (e.g. Semere & Slater, 2007a; Clapham & Slater, 2008; Bellamy et al., 2009; Bourke et al., 2013; Stanley & Stout, 2013). Given that commercial Miscanthus cultivation is comparatively new to agriculture, predominantly very young Miscanthus fields have been studied so far, in which crop cover can be very patchy (Lewandowski et al., 2000; Price et al., 2004; Atkinson, 2009). Over time, gaps should become filled with Miscanthus stems as the rhizomes spread (Lewandowski et al., 2000; Clapham & Slater, 2008), and in future, improved planting technology and increased domestication (Karp & Shield, 2008; Karp & Richter, 2011) may reduce patchiness, and alter the effects of Miscanthus on within-crop biodiversity.

In Ireland, a country that has significant potential for bioenergy production, Miscanthus has gained interest from the farming community and researchers alike (Clifton-Brown et al., 2000; Dieterich et al., 2008). However, patchiness often remains in commercial fields, even 4 years after planting (Zimmermann et al., 2013), and the expected breakdown of the initial planting structure and closure of gaps (Lewandowski et al., 2000) does not always occur. Miscanthus crop patchiness has economic implications for farmers because patchiness has an impact on payback time for initial investments and might reduce gross margins by more than 50% (Zimmermann et al., 2013). In particular, systems where baseline yields are already low might not be able to achieve positive gross margins (Zimmermann et al., 2013). Therefore, if patchiness means that yields stay below the expected 8–15 t dry matter (d.m.) ha^{-1} yr^{-1} (Teagasc, 2008), they might drop below a threshold of economic viability for the mature crop, making Miscanthus uncompetitive with virtually all other productive uses of land in Ireland (Styles et al., 2008).

For commercial Miscanthus cultivation, we expected management to maximize yield to have an important impact on the species-level farmland biodiversity value of the respective fields. We studied fields that were 4–5 years old and therefore on the verge of crop maturation with respect to yield development. In Ireland, Miscanthus is either planted on arable land or improved grassland. The previous land use (PLU) could potentially affect both biodiversity and crop establishment (but see Bourke et al., 2013 and Zimmermann et al., 2013), and therefore we selected Miscanthus fields of both types of origin for our study. To test the effect of crop patchiness and hence yield on farmland biodiversity within those fields, we investigated species richness and cover of noncrop vegetation and selected invertebrate groups in plots varying in crop cover. Our findings may provide perspective on how biodiversity might develop as Miscanthus crops become denser due to improved cultivation experience. We discuss our results in the light of a potential trade-off between benefits for farmland biodiversity and accomplishment of climate change mitigation targets.

Materials and methods

Study sites

Commercial Miscanthus fields, located in south-eastern Ireland within areas of high potential Miscanthus × giganteus productivity (Clifton-Brown et al., 2000), were selected for sampling. In total, 14 fields were chosen; one field per farm, established via rhizome planting on previous grassland (MG; N = 7) and on previous tilled arable land (MT; N = 7) in 2006 and 2007. Field size (FS) ranged from 1.0 to 7.8 ha with an average FS of 3.7 ha. All sites were on sandy loam or loamy sand soils, pH-levels ranging from 5.3 to 6.8 and elevation ranging from 13 to 115 m asl.

Assessment of crop patchiness

When field work commenced in 2010, no high-resolution remote sensing pictures of the field sites were available. Therefore, the crop cover of field sites was assessed on the ground. Geographic (GPS) coordinates for the full perimeter of each field were recorded in May 2010 using a Mobile Mapper (CE Thales; Magellan MobileMapper CE GPS receiver (ArcPad 7.0)) to calculate the size of the respective fields. To determine the patchiness within the fields, transects of 200 m in length were mapped in each field. Where field dimensions allowed, the total transect was split into two parallel transects of 100 m

length, 50 m apart. For a number of fields, walking a higher number of shorter transects was necessary and for the smallest sites (1.0 and 1.3 ha), only two 80 m transects were possible. To avoid edge effects, transects were located at least 10 m from the field perimeter. Every 10 m along the transect, the presence or absence of any open patches in the crop intersecting the transect line were recorded, giving 20 recording points per transect. When patches were present at recording points, patch perimeters were recorded with the Mobile Mapper (see above) to map patch area and shape. Ten of the patches per field were subsequently chosen for further measurements of light penetration (LP), estimation of crop yield and biodiversity sampling.

Measurement of light levels in the crop

A basic photometer was used to measure the illuminance (lux) above the Miscanthus canopy and the incident light levels at the height of the ground vegetation canopy in late August 2010. Mean illuminance levels were calculated from three lux measurements at each level. Light penetration to the lower canopy level was calculated as a percentage of the total illuminance. An attempt was made to measure photosynthetically active radiation (PAR; McCree, 1981) at the lower canopy level within the Miscanthus patches using a SunScan system (SS1, DeltaT Devices Ltd, Cambridge, UK). This system allows PAR measurements to be taken along a 1 m sensor at ground or lower canopy level, while levels of incident radiation are simultaneously measured above the crop using a beam fraction sensor (BFS1, DeltaT Devices). The nature of the equipment and density and height of the Miscanthus crops in late season rendered full PAR recording infeasible; however, PAR measurements were attempted in four fields and PAR penetration was calculated. A regression analysis showed a highly significant relationship between $\log(\text{lux})$ and $\log(\text{PAR})$ ($t = 4.593$, df = 38, $P < 0.001$) and validated the use of the photometer measurements.

Miscanthus yield estimates

At the 10 sampling points along each transect, areas of 4 m in length and 20 cm in width were located perpendicular to the transect line with the mid-point of the area located on the transect, so that 2 m of the area protruded to the right and 2 m to the left of the transect. In total, the sampling area for counting and measuring of Miscanthus shoots was thus 8 m^2 per field, which is in excess of the recommended 5.6 m^2 for estimation of biomass yields in Miscanthus determined by Knörzer et al. (2013). All Miscanthus shoots within each area were counted. The mean height of Miscanthus stems within the sampling area was calculated from three measurements made with the use of an extendible rod and a tape measure.

Miscanthus yield of study fields was estimated by establishing a yield model based on data reported in Schwarz et al. (1995). Miscanthus yield (t d.m. ha^{-1}) was fitted as a linear function of shoot density (Miscanthus stems per m^2), shoot height (cm) and time since establishment (3 and 4 years; Schwarz et al., 1995). A model with shoot density and an interaction between height and time since establishment explained 86.6% of the variability in yield of the data taken from Schwarz

et al. (1995). The parameter coefficients of the yield model were used to predict the yields of our fields from the averages per study field of shoot density and Miscanthus height.

Vegetation survey

Plant species richness and vegetation cover were surveyed in 1 × 1 m quadrats at the 10 established measurement points per field. The centre point of each quadrat corresponded to an established sampling point on the transect line, with two sides of the quadrat running in parallel to the transect line. The percentage cover of each noncrop vascular plant species was recorded. Mosses and lichens were observed in some sites; however, their coverage was low and they were not included in this study. Percentage cover of noncrop vegetation was calculated by adding up the cover of the individual plants observed. Total vegetation cover may have exceeded 100% because plants overlap. The height of noncrop vegetation was measured using a metre rule at three points within the quadrat and a mean value calculated. Species classification and nomenclature are in accordance with Cope & Gray (2009) and Stace (2010).

Epigeic arthropod sampling

Ten pitfall traps were placed in each field. Due to the ground disturbance associated with the pitfall traps used for invertebrate sampling, the traps were not located within but at the bottom right-hand corner of the quadrats for vegetation survey, with bottom right hand being defined by the direction of the transect walk. Individual traps were ~20.3 cm in diameter and 20.3 cm in height. They were dug into the ground, rims placed at surface level and were filled to one third with an ethylene glycol solution (Schmidt et al., 2006). To prevent small mammals from entering the traps, a 1 cm mesh metal grid was wedged horizontally inside the opening of the trap. To protect the trap contents from dilution or overflowing from rainfall, a square lid of similar diameter to the trap was placed ~2 cm above the trap opening. All traps were placed on the 10th, 11th or 12th of June 2010 and then left for 7 days until collection on the 17th, 18th or 19th respectively. Hence, sampling conditions were as similar as possible for all traps and sites.

Collected specimens were sorted to a higher taxon level: Collembola, Coleoptera, Araneae, Hymenoptera, Diptera, Acarina, Hemiptera (Heteroptera and Homoptera), Diplopoda, Opiliones, Chilopoda, Isopoda, Dermaptera and Lepidoptera. Numbers of individuals per trap of those taxa were added up to get an estimate of the total activity density of arthropods during the trapping period. All ground beetles (Coleoptera: Carabidae) and spiders (Araneae) were identified to species level. Spider identification was based on Heimer & Nentwig (1991), Platnick (2012) and Roberts (1987, 1995); ground beetle identification was based on Luff (2007).

Data analyses

Separate general or generalized linear mixed effect models were performed for species richness and abundance of each

taxonomic group. Model family (i.e. probability distribution) for each dependent variable was selected based on model comparison of global models (see below) fitted with Gaussian, Poisson and negative binomial errors. The model family of the model with the lowest Akaike's Information Criterion (AIC) was used in subsequent analysis, which was Poisson errors and log link for species richness of plants, spiders and ground beetles; normal errors for vegetation cover and negative binomial errors and log link for the activity density of total epigeic arthropods, spiders and ground beetles. To maximize statistical power, data were analysed at the scale of sampling by including field ID as a random factor to account for the spatially repeated within-field sampling design, i.e. 10 traps or quadrats within each field.

Model variables included the fixed effects PLU (MG/MT), % LP and FS (ha) for analysis on vegetation. Models for analysis of epigeic arthropods included PLU (MG/MT), vegetation cover (mean centred), patch area (log-transformed) and FS (ha). As patch area and LP were highly correlated (Fig. S1 and Table S2), we decided a priori to include % LP for analysis on vegetation, because we considered LP to have a more immediate effect on vegetation in comparison with patch area.

For model selection, first, a global model was generated that contained all fixed effects and two-way interaction terms. Then, special cases of the global model (candidate models), which included subsets of explanatory variables, were specified and compared using dAIC and Akaike weights w_i. The latter can be interpreted as the probability that the selected model is the best model of those considered. For model comparisons, mixed effect models were fitted with maximum likelihood (ML, when possible) and refitted with restricted maximum likelihood to evaluate parameter estimates, which were averaged across models with dAICc <2 or <null model (Burnham & Anderson, 2002). Model averaging was done with shrinkage, i.e. in models where, a variable is absent, the corresponding coefficient is set to zero (Burnham & Anderson, 2002). Hence, this method decreases effect sizes of variables that do only occur in models with low w_i and does not have a tendency of biasing the value away from zero. To assess the relative importance of each predictor variable, the sum of Akaike weights $w+(j)$ was calculated, by summing w_i over all models in the set that contain the predictor variable (Burnham & Anderson, 2002). Hence, $w+(j)$ measures the proportion of the set of models that contain that variable and the larger $w+(j)$, the more important is the variable of interest in comparison with other variables. Results for predictor variables with a sum of Akaike weights below 0.5 are presented in the supplementary material (Fig. S2). Model appropriateness was assessed by plotting residuals (when possible) vs. fitted values and vs. explanatory variables, respectively, and by normal QQ-plots.

In a second analysis, we tested whether species richness and abundance of each taxonomic group differed between fields of crop yields above or below the economic threshold of Miscanthus productivity. Styles et al. (2008) calculated that a reduction below 9.8 t d.m. ha^{-1} yr^{-1} peak harvested yield would see annualized discounted gross margins reduced to just EUR 40 ha^{-1} without subsidies, making Miscanthus uncompetitive with virtually all other productive uses of land in Ireland.

Richter et al. (2008) assessed an economic threshold of 9 t ha^{-1} for the United Kingdom. Generalized and general linear models were fitted on the components of biodiversity (as above) with Miscanthus yield (above or below the Irish threshold of 9.8 t ha^{-1} [Styles et al., 2008]) and the PLU (MG/MT), and the interaction term as predictor variables. Models with different sets of predictor variables were compared via dAICc or dQAICc. The model with the lowest AICc or QAICc was regarded to be the best fit and was used for interpretation. Separate analyses at field level ($n = 14$) were done for species richness of plants, vegetation cover of noncrop plants, activity density of epigeic arthropods, activity density and species richness of spiders and ground beetles respectively.

All statistical analysis was done in R (2012) [using libraries glmmADMB (Fournier et al., 2012), lme4 (Bates et al., 2013), nlme (Pinheiro et al., 2013), MASS (Venables & Ripley, 2002) and MuMIn (Barton, 2013)]. In the text, arithmetic mean and SD is given.

Results

Miscanthus yield and patchiness

The size of open patches in the crop cover measured along the transect lines was highly variable (Table 1). Both patch size and LP tended to be larger in Miscanthus established on grassland (MG) than in Miscanthus established on tilled arable land (MT), but differences were not significant (Table 1).

The predicted Miscanthus yield ranged from 5.8 to 13.8 t d.m. ha^{-1} yr^{-1} (Table 1). The upper end of this range lies well within the expected range for Ireland of 8–15 t d.m. ha^{-1} yr^{-1}. Three of the 14 fields investigated, however, had yields below the lower end of the expected yield range (one of MT; two of MG). None of the yields were above the upper expected yield level for Ireland of 15 t d.m. ha^{-1} yr^{-1}. Eight fields had yields below the economic threshold of 9.8 t d.m. ha^{-1} yr^{-1} (four of MT; four of MG) and six fields had yields above the economic threshold.

Vegetation

In total, 72 different vascular plant species were observed, comprising 46 forbs, 14 grasses, 6 sedges and 6 woody plants. The plant species richness and the vegetation cover of noncrop plants in individual patches showed similar ranges for both MT and MG (Table 1).

Light penetration was the most important factor for both plant species richness and vegetation cover, followed by PLU and FS (the latter for vegetation cover only; Table 2). Plant species richness and vegetation cover increased with increasing LP and were lower on MT compared with MG (Table 3, Fig. 1). The

Table 1 Summary statistics and p value for the comparison of Miscanthus fields established on tilled land (MT) and established on grassland (MG). Significance levels were obtained from mixed effect models for patch level data or from ANOVA for field level data (i.e. field size and yield). Data were log- or square root-transformed (when necessary) to achieve normally distributed residuals. Note that results of this one-factorial test may change when covariables are included in the model (see Supplementary materials: Table S3)

| | Miscanthus fields established on | | | | |
| | Tilled land (MT) | | Grassland (MG) | | |
	Mean ± SD	Range	Mean ± SD	Range	P-value
Patch area [m²]	10.1 ± 7.15	0.07–43.50	16.3 ± 28.32	1.55–212.88	0.728
Light penetration [%]	23.5 ± 18.65	1.20–94.58	31.0 ± 24.99	2.85–96.16	0.473
Field size (ha)	4.4 ± 2.13	2.0–7.9	2.9 ± 1.43	1.0–4.9	0.181
Yield [t dry mass ha⁻¹ yr⁻¹]	9.6 ± 1.60	7.50–12.00	9.4 ± 2.70	5.80–13.80	0.887
Plant species richness [per 1 m²]	4.7 ± 2.19	1–11	5.2 ± 2.25	1–11	0.532
Vegetation cover [%]	86.4 ± 57.82	2–245	125.7 ± 50.48	5–273	0.103
Activity density of total arthropods [per trap]	103.1 ± 57.62	31–303	113.9 ± 84.89	8–480	0.981
Activity density of spiders [per trap]	14.9 ± 7.17	1–30	13.1 ± 6.89	1–32	0.464
Species richness of spiders [per trap]	5.5 ± 1.83	1–10	5.5 ± 2.12	1–10	0.982
Activity density of ground beetles [per trap]	16.4 ± 16.18	1–89	15.1 ± 12.02	1–54	0.931
Species richness of ground beetles [per trap]	5.4 ± 3.07	1–12	5.6 ± 2.71	1–12	0.859

Table 2 The relative importance of predictor variables w+(j) expressed as the sum of Akaike weight across all models to explain species richness and activity density (or cover) of plants, all epigeic arthropods, spiders and ground beetles. w+(j) is a measure of the relative importance of predictor variables, and measures the proportion of the set of models that contain that variable (Burnham & Anderson, 2002; as a main effect or interaction). NA: parameter was not included in the models

| | Plants | | Epigeic arthropods | Spiders | | Ground beetles | |
	Species richness	Vegetation cover	Activity density	Activity density	Species richness	Activity density	Species richness
Previous land use (PLU)	0.22	0.88	1.00	0.85		1.00	0.28
Light penetration (LP)	1.00	1.00	NA	NA	NA	NA	NA
Vegetation cover (VC)	NA	NA	1.00	1.00		1.00	0.65
Patch area (PA)	NA	NA	0.36	1.00			0.12
Field size (FS)		0.73	1.00	0.46		1.00	0.87
PLU × LP		0.27	NA	NA	NA	NA	NA
PLU × VC	NA	NA	1.00	0.48		1.00	
PLU × PA			0.19				
PLU × FS		0.30	0.23	0.08		1.00	
VC × PA				1.00			

interactions in the model for vegetation cover indicate a lower difference in vegetation cover between MT and MG at high LP (Fig. 1b). Vegetation cover increased with FS with stronger increases in MG than MT (Fig. 1c). However, relative importance and effect sizes of PLU for plant species richness and the interaction between PLU and LP for vegetation cover were small in comparison with LP and hence are hardly apparent in prediction lines obtained from model averaging in Figure 1a and b.

Epigeic arthropods

A total of 15 188 individual specimens were collected and identified to higher taxon level. The total number of specimens found on the MT fields was 7214 and on the MG fields 7974. The most abundant taxa found were Collembola (47% of the total number of individuals), Coleoptera (23%) and Araneae (18%). Similar activity density of all arthropods, spiders and ground beetles, and species richness of spiders and ground beetles were found between MG and MT (Table 1).

The activity density of all epigeic arthropods was positively related with vegetation cover in MG, but slightly negatively related in MT (Fig. 2a) and increased with FS (Fig. 2b). The activity density of spiders was positively related with vegetation cover (particularly in MG) and patch size. Only at high levels of vegetation cover did the activity density of spiders on MG match those on

Table 3 The averaged coefficients of the predictor variables included in the best subset models as in Table 2. NA: parameter was not included in the models

	Plants		Epigeic arthropods	Spiders		Ground beetles	
	Species richness	Vegetation cover	Activity density	Activity density	Species richness	Activity density	Species richness
Intercept	1.42	53.87	4.27	2.42	1.69	2.42	1.33
Previous land use (PLU)	−0.022	−11.55	−0.06	0.15		−0.86	−0.001
Light penetration (LP)	0.005	0.55	NA	NA	NA	NA	NA
Vegetation cover (VC)	NA	NA	0.005	0.009		0.009	0.001
Patch area (PA)	NA	NA	−0.006	0.10			−0.005
Field size (FS)		18.66	0.11	−0.02		0.003	0.09
PLU × LP		0.16	NA	NA	NA	NA	NA
PLU × VC	NA	NA	−0.006	−0.001		−0.009	
PLU × PA			−0.03				
PLU × FS		−12.44	−0.007	0.002		0.24	
VC × PA				−0.003			
Model R²	3.5	27.6	30.3	12.6		44.6	26.1

MT (compare solid lines of Fig. 2c with d). The interaction between vegetation cover and patch size showed that highest densities of spiders occurred either in small patches with high vegetation cover or large patches with low vegetation cover (Fig. 2c and d).

The activity density of ground beetles increased with vegetation cover in MG, but not in MT (Fig. 3a). Differences in the activity density of ground beetles between MT and MG are apparent at low vegetation cover only. Activity density of ground beetles increased with FS in MT, but not in MG (Fig. 3b). Species richness of ground beetles increased with increasing vegetation cover (Fig. 3c) and increasing FS (Fig. 3d) and was only marginally higher in MG compared with MT.

Relationship between yield and biodiversity

On fields with yields above the economic threshold, plant species richness and activity density of spiders was marginally lower than on fields with yields below the economic threshold (Table 4, Fig 4a and c; summaries of models are presented in Table S4). This pattern was irrespective of PLU (Table 4). For vegetation cover and activity density of ground beetles, interactions between yield and PLU were ascertained (Table 4). On MG fields with yields above the economic threshold, vegetation cover and activity density of ground beetles were lower than on MG fields with yields below the economic threshold (Fig. 4b and d). On MT fields, in contrast, activity density of ground beetles was higher on fields with yields above the economic threshold (Fig. 4d). A comparable trend observable for vegetation cover was not verified by the model. No significant differences between fields of different yield levels were observed for activity density

of all arthropods and species richness of spiders and ground beetles.

Discussion

Commercially used Miscanthus fields in Ireland often retain a patchy crop cover with individual gaps of up to 213 m² in area, even after the establishment phase (see also Zimmermann *et al.*, 2013). Plant species richness and noncrop vegetation cover in Miscanthus fields increased with increasing patchiness, due to higher levels of LP to the lower canopy in the open patches. The activity density of arthropods and in particular of spiders and ground beetles followed the increase in vegetation cover and thus indirectly depended on crop patchiness. Those relationships were in several cases modulated by PLU and patch area. Comparatively low levels of plant species richness, vegetation cover and activity density of spiders and ground beetles were found for Miscanthus fields with yield levels above the economic threshold of Miscanthus production in Ireland (Styles *et al.*, 2008). But again, PLU had an important modulating effect on those relationships, in particular for activity density of ground beetles.

Light is often identified as one of the major factors influencing phytodiversity in biomass crop plantations (Gustafsson, 1987; Archaux *et al.*, 2010; Baum *et al.*, 2012a,b). In Miscanthus, in particular during the first 3–5 years of the establishment phase, light availability to the lower canopy depends on the patchiness of crop cover and planting density (Clifton-Brown *et al.*, 2000; Karp & Shield, 2008). In addition, annual harvest in spring and late emergence of new shoots (Haughton *et al.*, 2009) create an annual period of low vegetation height and bare ground, which may provide suitable
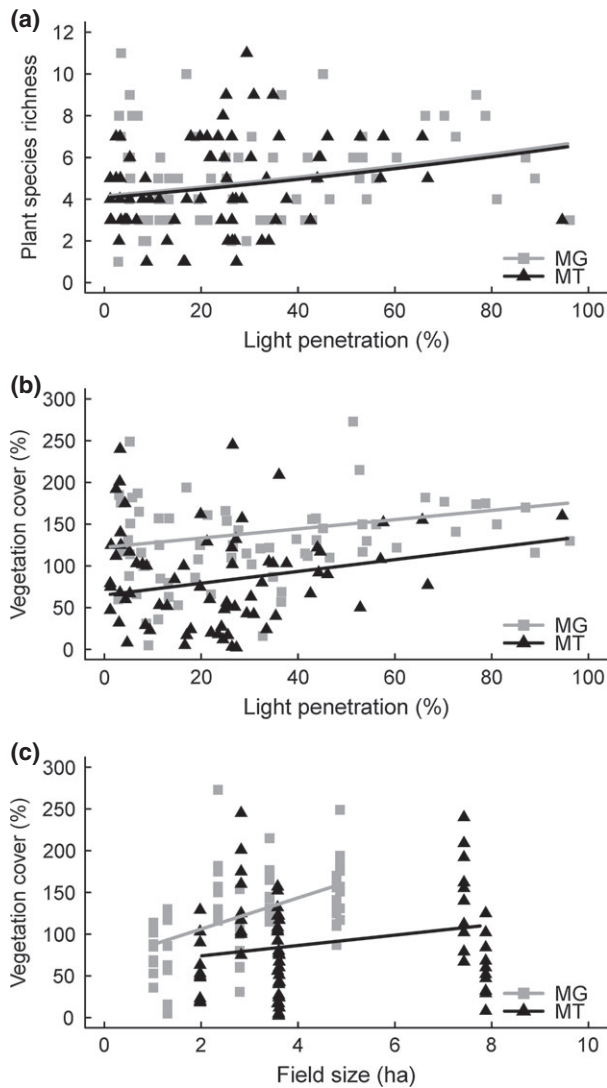
Fig. 1 Positive relationship between (a) plant species richness per quadrat, (b) vegetation cover (%) with light penetration and (c) between field size and vegetation cover for Miscanthus established on previous grassland (MG; N = 70 plots) and Miscanthus on previous tillage (MT; N = 70 plots). Prediction lines are obtained from averaged model coefficients (with shrinkage) in Table 2.

habitat for arable weed species adapted to early and short growth periods (Semere & Slater, 2007a; Bellamy et al., 2009). Our study corroborated the importance of LP within the crop for both plant species richness and noncrop vegetation cover. The noncrop flora of the Miscanthus fields studied here did not contain species typical of woodlands, which are able to exploit low-light conditions (see Table S1 for the list of plant species found), contrary to studies from SRC plantations (e.g. Baum et al., 2012a). This may well be due to the annual cyclical nature of Miscanthus growth and harvest,

which requires that species that persist in the mature crop also survive the growth period during which they are exposed to virtually full incident light intensity following harvest. Previous land use also had an influence on plant cover, with MG having a higher vegetation cover than MT. This pattern might be due to subtle differences in the composition of noncrop vegetation communities, with grass species playing a more dominant role on previous grassland sites (mean percentage cover of grasses on MG was 65.7% compared to 39.3% on MT). The more distinct effect of FS on vegetation cover in MG fields may also be attributable to those differences in plant species composition and the legacy of PLU.

Epigeic arthropods, apart from activity density of spiders, did not appear to be directly affected by the presence of gaps within the Miscanthus canopy. The activity density of epigeic arthropods, spiders and ground beetles, as well as the species richness of ground beetles, was, however, indirectly affected by the vegetation cover in these open patches. On MG fields, spiders needed an increase in vegetation cover to reach the same level of activity density they showed on MT fields. Given that spiders are rapid colonizers of agricultural fields (Marc et al., 1999; Maloney et al., 2003), those differences are more likely to result from current differences between MG and MT than from the legacy of land-use past. Several studies have shown that habitats high in plant species structural complexity are associated with species-rich insect communities (Dennis & Fry, 1992; Asteraki et al., 1995). As invertebrates show complex dependencies on sward architecture and plant community composition (Asteraki, 1994; Woodcock et al., 2007), the subtle differences in vegetation cover and composition found between MT and MG sites make an interpretation of the response of spiders and ground beetles difficult. Differences in the cover of grass and forb species between MG and MT sites may partly be responsible as predatory species might show a tendency for higher abundances in swards with more flowers, which attract a higher number of potential prey species compared with grass-dominated swards (Meek et al., 2002). To ascertain such hypotheses, more in-depth studies of the sward architecture and prey availability in the patches would be necessary.

Semere & Slater (2007b) reported a high number of invertebrates in the weed flora within Miscanthus fields. They found ground beetles, butterflies and arboreal invertebrates to be more abundant and diverse in the most floristically diverse Miscanthus fields. For the ground beetles, better microenvironmental conditions in the weed layer for reproduction and larval survival, as well as better food resources for adult beetles (i.e. weed-seed diet and herbivorous invertebrate diet) were
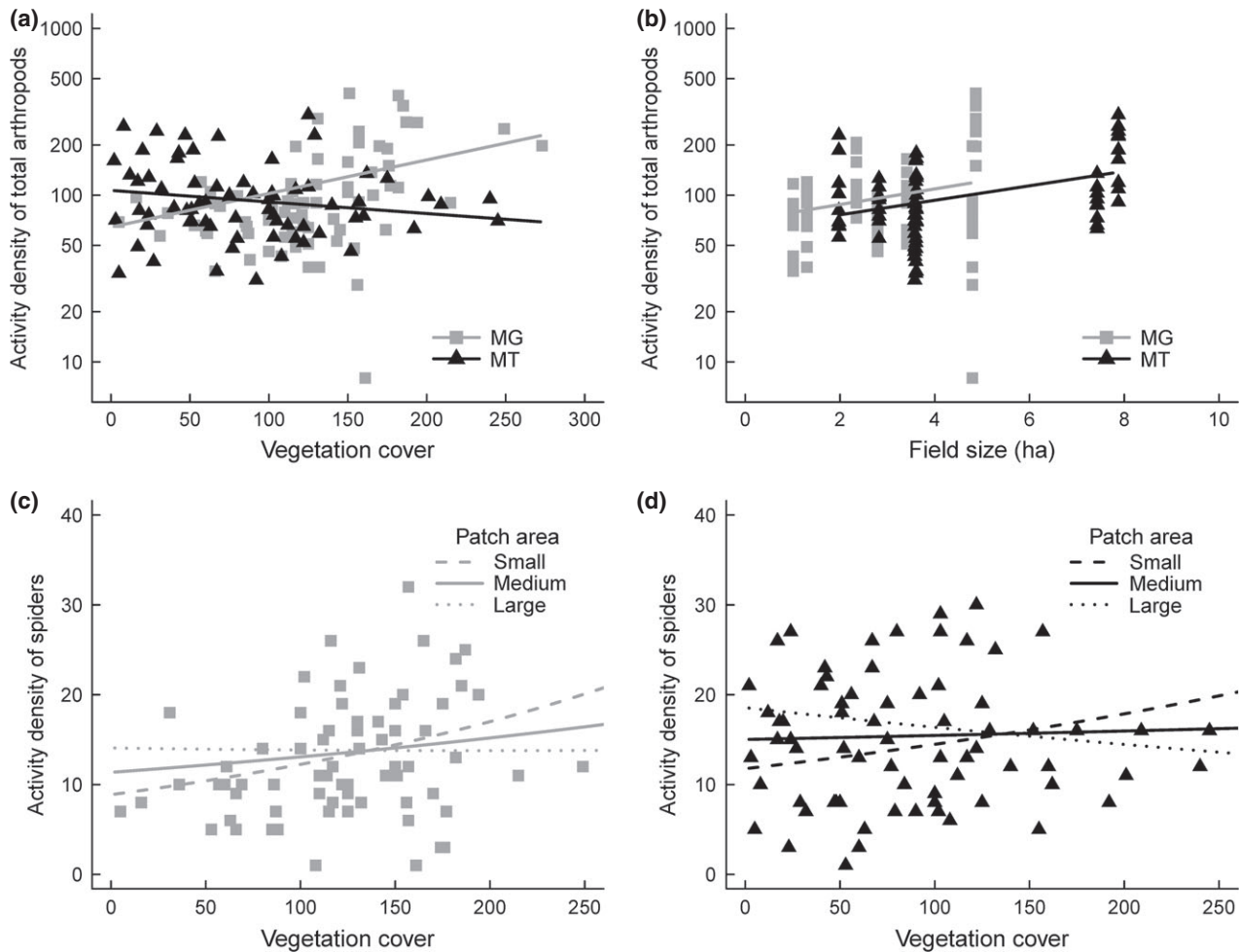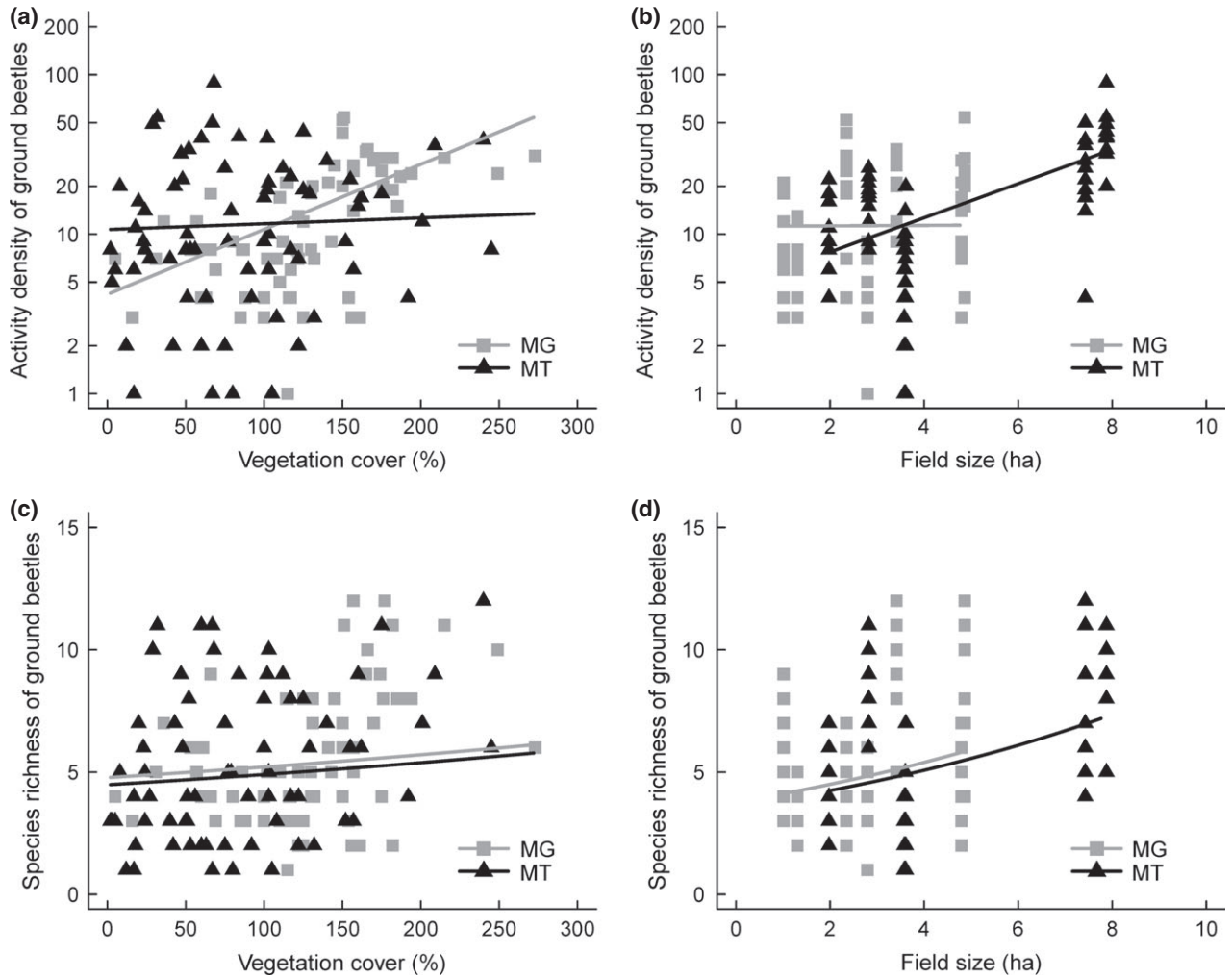
Fig. 2 Relationship between activity density of total arthropods per trap with (a) vegetation cover (%) and (b) field size (ha) for Miscanthus established on previous grassland (MG; $N = 70$ plots) and Miscanthus on previous tillage (MT; $N = 70$ plots). Relationship between activity density of spiders per trap with vegetation cover (%) for Miscanthus established on previous grassland (c) and Miscanthus on previous tillage (d). Prediction lines are obtained from averaged model coefficients (with shrinkage) in Table 2.

suggested as beneficial factors (Semere & Slater, 2007b). From afforested habitats, it is reported that stands with a more open canopy and hence a high vegetation cover in the field layer support a high richness of both open-specialist and total spider species (Oxbrough *et al.*, 2005) as well as positively affecting ground beetle diversity (Day *et al.*, 1993). Greater vegetation structure may offer increased protection from predators and places to conceal themselves from prey (Uetz, 1991), but at the same time provide greater availability of prey in the structurally diverse open areas (Oxbrough *et al.*, 2006). Larger prey items, in particular, may become more available to relatively large active hunters such as the spider *Pardosa pullata* (Oxbrough *et al.*, 2006), which was among the most numerous species in our study. The situation for ground dwelling arthropods in open patches within the Miscanthus fields mirrors relationships between vegetation cover and epigeic arthropods observed from field margins or perhaps set aside land (see, e.g. Woodcock *et al.*, 2007).

Plant species richness and activity density of spiders on both MT and MG fields, as well as vegetation cover and activity density of ground beetles on MG fields, were negatively associated with Miscanthus yield. Those patterns were to be expected from the results reported for the patches within the fields. In MT fields, however, activity density of ground beetles was higher in higher yielding fields and a comparable tendency was observable for vegetation cover. Those unexpected patterns might be due to interdependencies between yield, FS and activity density of ground beetles and vegetation cover because latter increased with size of MT fields, and the two largest fields also had the highest yields.
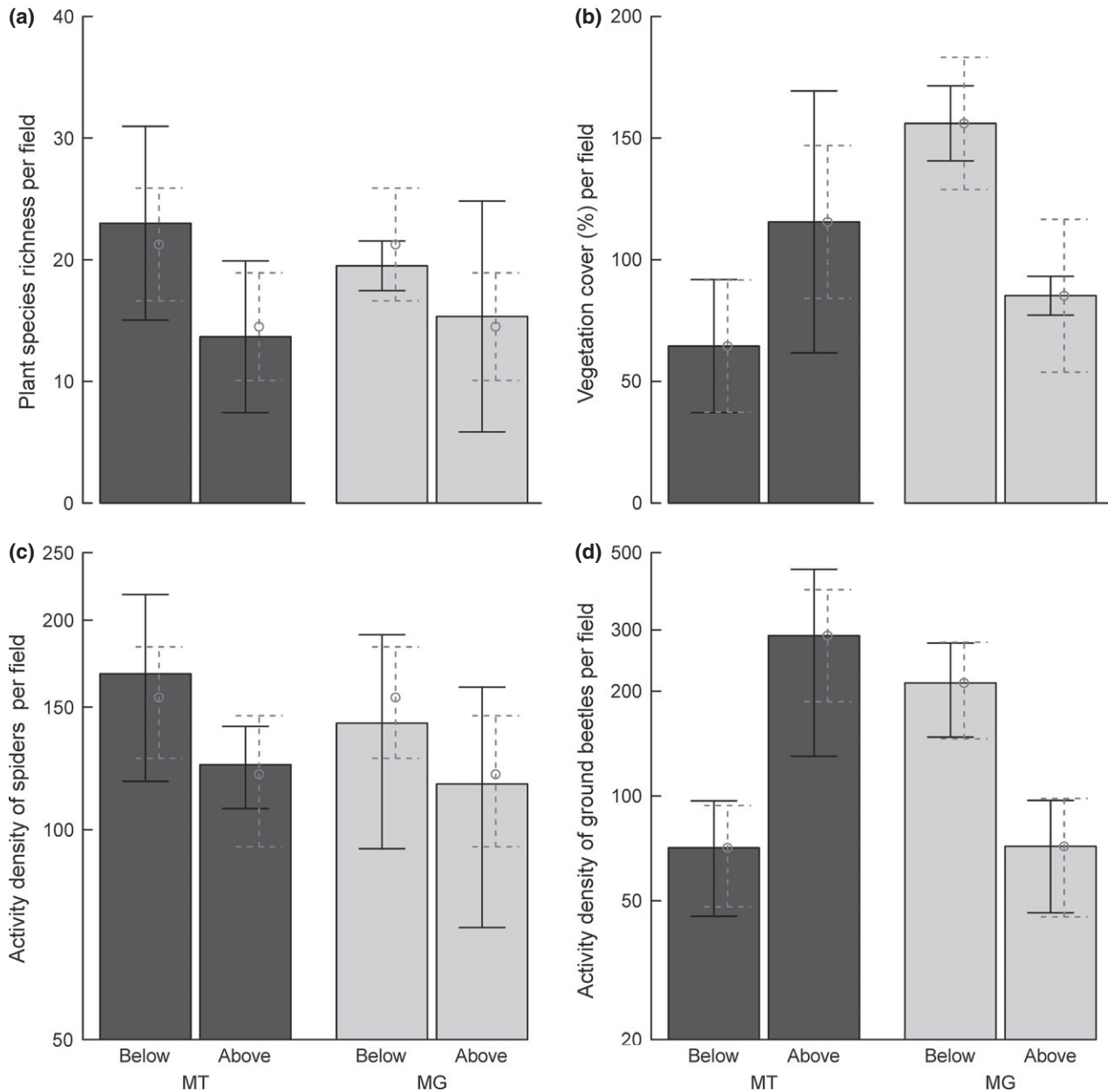
Fig. 3 Relationship between activity density and species richness of ground beetles, respectively, per trap with (a and c) vegetation cover (%) and (b and d) field size (ha) for Miscanthus established on previous grassland (MG; $N = 70$ plots) and Miscanthus on previous tillage (MT; $N = 70$ plots). Prediction lines are obtained from averaged model coefficients (with shrinkage) in Table 2.

Table 4 The parameter coefficients of the predictor variables, the model R^2 and model family are given for the best models examining the relationship between components of biodiversity and crop yield above or below the economic threshold ($N = 14$ sites). Model R^2 was assessed by the correlation between predicted and observed values

	Plants		Epigeic arthropods	Spiders		Ground beetles	
	Species richness	Vegetation cover	Activity density	Activity density	Species richness	Activity density	Species richness
Intercept	2.674	115.5		4.79		5.67	
Previous land use (PLU)		−30.3				−1.394	
Yield (Y)	0.382	−51.0		0.254		−1.404	
PLU × Y		121.9				2.485	
Model R^2	26.2	70.6		17.1		67.7	
Family	Quasi-poisson	Gaussian		Negative binomial		Negative binomial	

Levels of plant species richness reported from fields yielding more than 9.8 t d.m. ha^{-1} yr^{-1} in our study correspond to levels of plant species richness reported for conventional wheat fields in the same study region by Bourke *et al.* (2013). The finding that Miscanthus fields harbour higher plant species richness than

Fig. 4 Relationship between (a) plant species richness per field, (b) vegetation cover (%), (c) activity density of spiders per field and (d) activity density of ground beetles per field with crop yields below or above the economic threshold for Miscanthus established on previous grassland (MG; $N = 7$ sites) and Miscanthus on previous tillage (MT; $N = 7$ sites). Dark and light grey bars represent means of observed values on MT and MG respectively. Confidence intervals (mean ± 1.96 SE) of observed values are shown in black solid lines and of model predictions in grey dashed line. For model summary, see Table 4.

conventional wheat fields (Semere & Slater, 2007a; Bellamy et al., 2009) might thus only be true for comparisons with fields of low Miscanthus yield. Negative relationships between yield and biodiversity have so far been found for cereal farming systems (Geiger et al., 2010; Gabriel et al., 2013). Gabriel et al. (2013) showed that positive effects on biodiversity in organic systems occur mainly due to lower yields, but that benefits

diminish when yields reach levels of 'average' conventional farming.

We estimated an average Miscanthus yield of 9.6 t d.m. ha^{-1}, which is equal to the overall national average dry matter yield in the United Kingdom (Richter et al., 2008), and is well within the range of 8–15 t d.m. ha^{-1} yr^{-1} expected for Ireland (Teagasc, 2008). The estimated average yield from our data is very close to the

economic threshold values calculated by Styles *et al.* (2008) and Richter *et al.* (2008), indicating that for some of the farms, returns from Miscanthus production, might not be competitive to alternative uses of land. Improved yields of commercial Miscanthus production are therefore a necessity to make Miscanthus an economically viable crop as well as establish Miscanthus as a significant biomass provider for cofiring in Ireland. The current cultivated area of Miscanthus will only supply a fraction of the biomass required to meet Ireland's 30% cofiring target by 2015 (Caslin *et al.*, 2010). Consequently, there is a need to further increase energy biomass production (Augustenborg *et al.*, 2012). If yields dip below the margins promised to the farmers by farming advisors or contractors, there is a risk of disappointing farmers' expectations and in consequence reduce their willingness to adopt the energy crop. Indeed, suitability for marginal land and high productivity were regarded as convincing arguments for taking up Miscanthus cultivation by potential adopters of Miscanthus among farmers in Ireland (Augustenborg *et al.*, 2012). If, as suggested by some of our data, farmland biodiversity at the species level is directly or indirectly linked to Miscanthus productivity, biodiversity benefits are likely to diminish. Comparable trends have been reported for other biomass feedstock as well. Positive effects of switchgrass cultivation on the occurrence of beneficial insects reported by Gardiner *et al.* (2010), for example, depended on the vegetation diversity of the sites, which could be diminished by management of higher intensity. Overall, this indicates a trade-off between goals of climate change mitigation, which depend on sufficient biomass yields and biodiversity conservation within the bioenergy sector.

In conclusion, caution is advised when assessing the wildlife friendliness of biomass crops, in particular when looking at relatively novel perennial crops and inchoate cropping systems. A lack of experience in crop establishment, lower management intensity and low levels of crop domestication may lead to patchy crop cover in the establishment phase and increasing habitat suitability for associated biodiversity. Thus, early estimations of biodiversity value may not be maintained at the intensity levels of fully established cropping systems. The necessity to manage biomass crops for high yields, to meet energy and climate change mitigation targets, might diminish positive effects on biodiversity once a full-scale commercial production of the crop has been established.

Acknowledgements

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Supporting Information

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

Figure S1. Matrix plot of patch area, light penetration and vegetation cover Miscanthus established on previous grassland (MG) and Miscanthus on previous tillage (MT).

Figure S2. Relationship between activity density of total arthropods per trap and patch area (a) and between activity density of spiders and field size (b) for Miscanthus established on previous grassland (MG) and Miscanthus on previous tillage (MT).

Table S1. Lists of plant, spider and ground beetle species found on all study sites.

Table S2. Correlation matrix for covariables used in mixed effect models describing the patches on 14 Miscanthus fields established on tilled land and grassland.

Table S3. Best candidate models with ΔAICc <2 and null and global model explaining species richness of plants, vegetation cover of noncrop plants, activity density of epigeic arthropods, activity density and species richness of spiders and ground beetles respectively.

Table S4. Summary of generalized and general linear models explaining species richness of plants, vegetation cover of noncrop plants, activity density of epigeic arthropods, activity density and species richness of spiders and ground beetles at field level by previous land use (PLU) and crop yield below or above the economic threshold (Yield) and their interaction.