50 YEARS WITH IMPACT Journal of Applied Ecology 1913 British Ecological Society 2013 CELEBRATING 100 YEARS

Journal of Applied Ecology 2013, **50,** 355–364 doi: 10.1111/1365-2664.12035

Food production vs. biodiversity: comparing organic and conventional agriculture

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Summary

1. A substantial proportion of the global land surface is used for agricultural production. Agricultural land serves multiple societal purposes; it provides food, fuel and fibre and also acts as habitat for organisms and supports the services they provide. Biodiversity conservation and food production need to be balanced: production needs to be sustainable, while conservation cannot be totally at the expense of crop yield.

2. To identify the benefits (in terms of biodiversity conservation) and costs (in terms of reduction in yields) of agricultural management, we examined the relationship between crop yield and abundance and species density of important taxa in winter cereal fields on both organic and conventional farms in lowland England.

3. Of eight species groups examined, five (farmland plants, bumblebees, butterflies, solitary bees and epigeal arthropods) were negatively associated with crop yield, but the shape of this relationship varied between taxa. It was linear for the abundance of bumblebees and species density of butterflies, concave up for the abundance of epigeal arthropods and butterflies and concave down for species density of plants and bumblebees.

4. Grain production per unit area was 54% lower in organic compared with conventional fields. When controlling for yield, diversity of bumblebees, butterflies, hoverflies and epigeal arthropods did not differ between farming systems, indicating that observed differences in biodiversity between organic and conventional fields are explained by lower yields in organic fields and not by different management practices *per se*. Only percentage cover and species density of plants were increased by organic field management after controlling for yield. The abundance of solitary wild bees and hoverflies was increased in landscapes with high amount of organic land.

5. *Synthesis and applications*. Our results indicate that considerable gains in biodiversity require roughly proportionate reductions in yield in highly productive agricultural systems. They suggest that conservation efforts may be more cost effective in low-productivity agricultural systems or on non-agricultural land. In less productive agricultural landscapes, biodiversity benefit can be gained by concentrating organic farms into hotspots without a commensurate reduction in yield.

Key-words: agri-environment schemes, agro-ecology, conservation, diversity, land sharing, land sparing, landscape, organic farming, wheat, yield

Introduction

The global demand for food and farmland is rapidly growing due to a variety of factors including rising human population numbers, increased meat consumption, urbanization, competing land uses for non-food crops and the alteration in the suitability of land to grow crops due to climate change (Tilman *et al.* 2009; Beddington 2010). While a reduction in food waste, improvements in infrastructure and transport, a change in human diets and expanding aquaculture are important mitigation strategies against increased demand (Godfray *et al.* 2010), it has

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been argued that agricultural production has to increase globally to supply the food required for the estimated over nine billion people by 2050 (Foresight 2011; Tilman *et al.* 2011). Increasing supply logically has two axes: either via intensification (increasing output over the same area) or via extensification (bringing more land into agricultural production). With agricultural intensification and land-use change being the major drivers for biodiversity loss, this will undoubtedly have a heavy impact on wildlife and the environment (Tilman *et al.* 2001).

Currently, two contrasting landscape-level scenarios are widely discussed with regard to preserving biodiversity while maintaining food production: wildlife-friendly farming ('land sharing') vs. land sparing (Green *et al.* 2005; Fischer *et al.* 2008). In a land-sparing scenario, the available land in a landscape is subdivided into some areas specialized for producing mainly agricultural produce, and others are devoted mainly to maintaining biodiversity and ecosystem services. This allows the agricultural land to be farmed intensively for high yields, while the spared land can be managed specifically for other services. There is no necessity for the 'spared land' to be spatially separated from the agricultural land; indeed, there are arguments that support it being a landscape-wide network of wildlife areas formed by field margins, small farm woodlands, water courses, etc. (Benton 2012). In the wildlife-friendly, land-sharing scenario the available land is under lower-intensity agriculture. The increased area of land in production compensates for its lower yield, and the decrease in intensity allows biodiversity to be conserved across the whole landscape. The optimal scenario depends on the shape of the yield vs. population density (or biodiversity) function (Green *et al.* 2005). If, from a high-yield baseline, a small reduction in yield causes a marked increase in biodiversity (a concave-down shape), then land sharing, or wildlife-friendly farming, is the better option. If, however, significant biodiversity gains require a very large reduction in yields (a concave-up shape), then land sparing is the better strategy. These contrasting scenarios should be considered as the endpoints of a continuum; it is not a question of 'either/or', but of how much of each strategy shall be applied and under what circumstances (Fischer *et al.* 2008). The solution is likely to depend on the peculiarities of populations, species groups or ecosystem services and the landscapes, regions or countries in focus (Hodgson *et al.* 2010).

In this study, we are interested in quantifying the trade-off between agricultural production and biodiversity. We recognize that impacts of farming are broader than biodiversity (e.g. environmental pollution and reduction in soil quality), and in theory, the sparing vs. sharing analysis could have a broader 'impacts vs. yield' trade-off. However, many reductions in ecosystem services are, by definition, mediated through species abundance and diversity, so examining this relationship in this instance is valuable. In the European context, different models have been used to describe the relationship between yield and biodiversity. Kleijn & Sutherland (2003) predicted that biodiversity will decline in a concave-up curve with agricultural intensity, a prediction recently supported by a study of farmland plants (Kleijn *et al.* 2009). This shape suggests that significant biodiversity is supported only when agricultural production is very low. A negative linear relationship between wheat yield and farmland bird species has been observed by Donald *et al.* (2006) and Geiger *et al.* (2010), which suggests that a reduction in agricultural intensity is equally effective at any yield. Hoogeveen, Petersen & Gabrielsen (2001) suggested a unimodal relationship, where biodiversity first increases and then declines as intensity increases. Under this scenario, the disturbance created by low-intensity farming leads to increased biodiversity relative to unmanaged land, but beyond an intermediate level of intensity biodiversity will decline.

Here, we focus on two farming systems, conventional intensive agriculture and organic farming – a specific example of wildlife-friendly agriculture. Organic farming is widely regarded as a more sustainable farming system than conventional agriculture because it produces food while conserving soil, water, energy and biodiversity (Pimentel *et al.* 2005), although 'sustainability' is a concept defined in many ways and with multiple currencies (e.g. greenhouse gas emissions, synthetic inputs, land use and biodiversity). Organic yields are globally on average 25% lower than conventional yields according to a recent meta-analysis (Seufert, Ramankutty & Foley 2012), although this varies with crop types and species and depends on the comparability of farming systems. Hence, it is questionable whether the environmental performance of organic farming is still better if related to the unit output per area.

We examine the impact of farming on biodiversity and ask two questions. First, in comparison with conventional farming, is organic farming beneficial for all biodiversity or differentially beneficial for different taxa and/or across different landscapes (Bengtsson, Ahnstrom & Weibull 2005; Hole *et al.* 2005)? Both the management of the farmland in the landscape, such as areas dominated by organic land, and the proportion of farming in the landscape, such as areas dominated by arable crops, can enhance or detract from the benefits of organic farming for different species groups (Holzschuh *et al.* 2007; Rundlof, Bengtsson & Smith 2008; Diekötter *et al.* 2010; Gabriel *et al.* 2010). Second, as crop yields are typically lower in organic compared with conventional farming systems (de Ponti, Rijk & van Ittersum 2012; Seufert, Ramankutty & Foley 2012), is the increase in biodiversity on organic farms sufficient to offset the necessary increase in total agricultural land that will be needed to increase the required crop yield? To our knowledge, few studies have contrasted crop yields of organic farming with biodiversity [see Ostman, Ekbom & Bengtsson (2003) for pest–natural enemy dynamics and Clough, Kruess & Tscharntke (2007) for staphylinids]. Thus, knowledge is very limited for the costs, in terms of yield loss, that are associated with biodiversity gains through organic farming in a wildlife-friendly farming scenario.

The aim of this study was to assess the trade-off between yield and biodiversity in both organic and conventional farms in lowland England. To reduce variation due to crop species, we focus in particular on winter cereal as Europe's most widespread arable crop. Biodiversity was assessed on a total of 165 fields of 29 farms in two regions over 2 years and measured as abundance and species density of plants, earthworms, insect pollinators (hoverflies, bumblebees and solitary wild bees), butterflies, epigeal arthropods (abundance only) and birds. Our expectation was that the shape of the negative relationship between biodiversity and yield might differ between taxa and farming systems. One might expect that taxa with limited mobility that use crop fields as their main habitat should respond more strongly than mobile multi-habitat users to crop yield. Furthermore, this response should follow a concave-down curve in organic fields if organic farming should be regarded as a wildlife-friendly farming system.

Materials and methods

STUDY DESIGN, CROP YIELD ESTIMATION AND BIODIVERSITY SURVEYS

The study design and the selection of fields, farms and landscapes are described in full detail in Gabriel *et al.* (2010). We selected sixteen 10 × 10 km landscapes, each containing paired organic and conventional farms. The 16 landscapes were arranged in eight clusters of paired landscapes. Four clusters were located in the Central South West and four in the North Midlands of England. Landscapes within a pair were chosen to have similar environmental conditions, but contrasting proportions of organic agriculture [hereafter called organic 'hotspots' for high (on average 17·2%) and 'coldspots' for low (on average 1·4%) proportions of organic land] (Gabriel *et al.* 2009). On each farm, three cereal fields were selected in 2007 and 2008. However, because crop yields and biodiversity may differ between spring and autumn-sown cereals, we chose only the winter cereal fields with wheat, oat and barley for this study, giving us 29 farms and 165 fields for comparison (16 farms with three fields each over 2 years = 96 conventional fields; and 13 farms with one to three fields each over 2 years = 69 organic fields).

Crop yield was estimated by taking the above-ground biomass of the crops from three 50 × 50 cm plots (25 m apart) from the field centres shortly before harvest. Samples were placed for 16 h in a drying oven at 70 °C, the wheat ears were threshed, and the grain was weighed. Hence, yield is measured as the grain's dry weight and is not equivalent to yields that farmer or agricultural statistics report because those differ in moisture content and include losses during harvest, transport and edge effects.

Farmland biodiversity was repeatedly surveyed during May–August in each year. Herbaceous vascular plant species (except grasses and ferns) were identified within quadrats, earthworms were sampled using the hot mustard method, epigeal arthropods were sampled with a Vortis suction sampler, flower visitors were assessed using pan traps, and butterflies and birds were recorded by walking standardized transects (for more details on biodiversity surveys see Appendix S1, Supporting information). All taxa were surveyed at the field level in the crop field centres (25 m into the cultivated area), except birds, which were recorded at the farm level (as standard transects covered multiple fields). Plants, earthworms and epigeal arthropods were also recorded in the field edges (0·5 m into the cultivated area), while butterflies and insect pollinators were recorded in the field margins (the uncultivated area). Field edges and margins are too close together for independent sampling of mobile taxa such as pollinating insects. Hence, in the analyses reported here, the crop edge or field margin assays are contrasted with field centre surveys to test the effects of within-field location.

STATISTICAL ANALYSIS

Farmland biodiversity was analysed in terms of abundance (percentage cover or number of individuals per area and/or time) and species density (number of species per area and/or time) of plants, earthworms, insect pollinators, butterflies, epigeal arthropods and birds. Generalized and general additive mixed effect models (GAMM) were fitted to test for linear and nonlinear relationships between components of farmland biodiversity and crop yield. Additive models fit a smoothing curve through the data and allow the data to define the appropriate shape of the curve, avoiding the need to specify a particular (parametric) curve. The smoothness of the curve is defined by its degrees of freedom (d.f.).

The statistical analysis was conducted in two steps. First, for each response variable we chose a modelling family based on its frequency distributions and model fit by specifying the error structure (normal, poisson and quasipoisson) with the respective link function (identity and log). We fitted biodiversity as a function of crop yield and accounted for the variability due to our hierarchical study design by including the random effects year (2007, 2008), survey in year (1–3), cluster (1–8), farm (1–29), field-within-farm (1–3) and location-within-field (1–2), when appropriate. To assess whether the relationship between measures of biodiversity and crop yield differed between the within-field location (centre vs. edge or margin), farm management (organic vs. conventional), landscape-scale management (hotspot vs. coldspot) and regions (Central South West vs. North Midlands), we allowed different smoother terms for the different factor levels (in essence, fitting an interaction term). We then compared models and dropping terms using AIC (QAIC for models with quasipoisson error) and also checked whether replacing the dropped interaction term with its equivalent main effect would improve the model fit. In the next step, we ran the best subset of models with d.f. of 2, 3 and 4 and compared their fit. All statistical analysis were conducted in R (R Development Core Team 2012).

Results

SUMMARY OF CROP YIELD AND BIODIVERSITY

Winter cereal yield in organic fields was 54% lower than in conventional fields (Table 1, Fig. 1a; see Supporting Analysis S2 (Supporting information) for a description of the farming practice and environment). In organic fields,

Table 1. Summary statistics describing crop yield and abundance and species density of different farmland taxa in conventional and organic winter cereal fields

	Conventional			Organic		
	Mean ± SEM	Median (range)	*n*	Mean ± SEM	Median (range)	*n*
Crop yield[a]	9·3 ± 0·25	8·9 (4·0–16·1)	96	4·3 ± 0·24	3·8 (1·4–11·1)	69
Plants (cover)[b]	1·5 ± 0·10	0·9 (0–84)	576	12·9 ± 0·75	16 (0–99)	414
Plants (species)[c]	2·5 ± 0·12	3 (0–18)	576	9·9 ± 0·34	11 (0–27)	414
Earthworms (individuals)[d]	2·1 ± 0·28	2 (0–24)	120	3·2 ± 0·45	3 (0–49)	88
Earthworms (species)[e]	1·1 ± 0·11	1 (0–6)	120	1·6 ± 0·15	2 (0–7)	88
Bumblebees (individuals)[f]	0·7 ± 0·03	1 (0–16)	1152	0·9 ± 0·04	1 (0–22)	828
Bumblebees (species)[g]	1·5 ± 0·08	2 (0–8)	384	1·9 ± 0·09	2 (0–9)	275
Solitary bees (individuals)[f]	0·8 ± 0·04	0 (0–22)	1152	0·8 ± 0·04	0 (0–26)	828
Solitary bees (species)[g]	1·2 ± 0·08	1 (0–12)	384	1·4 ± 0·10	1 (0–10)	275
Butterflies (individuals)[h]	1·9 ± 0·20	1 (0–59)	262	2·7 ± 0·31	2 (0–39)	188
Butterflies (species)[i]	1·1 ± 0·09	1 (0–9)	262	1·4 ± 0·12	2 (0–8)	188
Hoverflies (individuals)[f]	1·6 ± 0·07	1 (0–50)	1152	1·2 ± 0·06	1 (0–18)	828
Hoverflies (species)[g]	2·0 ± 0·11	2 (0–12)	384	1·9 ± 0·11	2 (0–14)	275
Epigeal arthropods[j]	8·6 ± 0·25	9 (0–92)	858	10·3 ± 0·37	11 (0–122)	633
Farmland birds (individuals)[k]	84·0 ± 5·06	77 (15–348)	95	91·4 ± 9·48	88 (18–1053)	69
Farmland birds (species)[l]	8·5 ± 0·22	8 (2–13)	95	7·8 ± 0·27	8 (2–14)	69

[a] tonnes ha^{-1}.
[b] % cover of all forb species per m^2 and survey and year.
[c] Number of forb species per 9 m^2 and survey and year.
[d] Number of adult individuals per 0·6 m^2 in 2007 and per m^2 in 2007.
[e] Number of species per 0·6 m^2 in 2007 and per m^2 in 2007.
[f] Number of individuals per pantrap and 48 h exposure.
[g] Number of species per three pan traps and 48 h exposure.
[h] Number of individuals per 15-min transect walk.
[i] Number of species per 15-min transect walk.
[j] Number of individuals per 45 s suction over 1·8 m^2.
[k] Number of individuals per 2-km transect walk.
[l] Number of species number of species per 2-km transect walk.

yield of winter wheat (4·2 tonnes ha^{-1}) was lower compared with winter oats (4·9 tonnes ha^{-1}) and winter barley (5·1 tonnes ha^{-1}).

Plants, earthworms, bumblebees, butterflies and epigeal arthropods had higher abundance and species densities in organic fields, while solitary bees had similar abundance in both farming systems and slightly higher species densities in organic fields. In contrast, hoverflies had higher abundance and species densities, and farmland birds had higher species densities in conventional fields (Table 1; see Gabriel *et al.* (2010) for more details on farmland biodiversity). Species density and abundance were closely related for all taxa (Fig. S4, Supporting information).

CROP YIELD VS. BIODIVERSITY

Farmland plants, bumblebees, solitary bees, butterflies and epigeal arthropods were all negatively associated with crop yield, hoverflies responded positively to yield (Figs 1b,c and 2, for model summaries see Table S4, Supporting information), while no significant relationship was observed for birds or earthworms.

For those species groups that were negatively associated with yield, the shape of the relationship differed between taxa. It was concave-down for percentage cover and species density of plants in organic fields (percentage cover in organic edges only) and for species density of bumblebees in field margins (Figs 1b,c and 2b). A linear relationship was observed for the abundance of bumblebees, species density of bumblebees in field centres and species density of butterflies (Fig. 2a,b,f). A concave-up relationship was observed for the abundance of butterflies in hotspots and for epigeal arthropods (Fig. 2e,i).

BIODIVERSITY IN ORGANIC AND CONVENTIONAL AGRICULTURE AFTER CONTROLLING FOR CROP YIELD

The overlap in observed yields in organic and conventional fields ranged from 4 tonnes ha^{-1} to 11 tonnes ha^{-1}, so we used this range of yields to predict biodiversity from our models. Across the species groups that had significant associations with yields, biodiversity was on average 100% higher in field edges or margins than in field centres, 35% higher in organic than in conventional fields, 6% higher in hotspots than in coldspots and 81% higher in the Central South West than in the North Midlands (Table 2). Examining each group separately, only plants show a biodiversity benefit from organic farming once yield is accounted for; cover was four times higher, and species density was doubled in

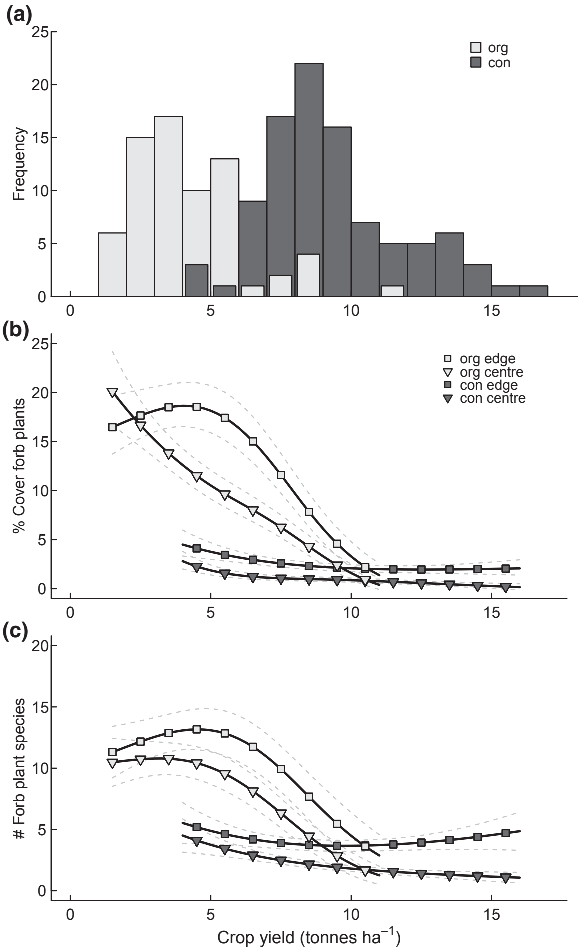

Fig. 1. (a) Frequency distribution of crop yield in 69 organic and 96 conventional winter cereal fields. Relationship between crop yield and (b) percentage cover and (c) species density of forb plants in field edges and centres of organic and conventional fields. Dashed grey lines represent range of predicted means ± standard errors.

organic compared with conventional fields. Abundance and species density of solitary bees were 33% and 19% lower, respectively, in organic fields at comparable yields, while the abundance and species density of bumblebees, butterflies and hoverflies, as well as the abundance of epigeal arthropods, did not differ between the two farming systems (Table 2). This shows that the differences in average numbers (Table 1) are explained by lower yields in organic fields and not by different management practices *per se*. Solitary bees and hoverflies had 34% and 27% higher abundance, respectively, in hotspots compared with coldspots, while butterflies only had higher abundance in hotspots at yields below 7 tonnes ha^{-1} (Fig. 2e).

BIODIVERSITY CHANGE THROUGH REDUCED CROP YIELD

According to our fitted models, where a field to be farmed in such a way to reduce yields from 10 tonnes ha^{-1} to 5 tonnes ha^{-1}, it would result in (i) a 355% gain in plant species in organic field centres and a 108% gain in conventional field centres; (ii) a 23% gain of bumblebee individuals and 20% and 7% gains of bumblebee species in field centres and margins, respectively; (iii) a 26% gain of solitary bee individuals, and a gain of solitary bee species of 21% in organic and 18% in conventional fields; (iv) a 119% and 59% gain of butterflies in field centres and margins in hotspot landscapes; (v) a 31% and 8% loss of hoverfly individuals and species in the North Midlands and (vi) a 18% gain of epigeal arthropods in field edges (see Table S5, Supporting information).

Discussion

The relationship between farming intensity, farming methods and their impact on wildlife is hugely important given the projected demand for increased global food production (Tilman *et al.* 2001; Foley *et al.* 2011; Foresight 2011; Tilman *et al.* 2011). Additionally, to guide effective conservation management, it is crucial to know how much agri-environmental management practices benefit biodiversity and how much they 'cost' in terms of reduced yield. We examined the relationship between diversity of important farmland taxa and crop yield on organic and conventional farms. Of eight species groups examined, five (farmland plants, solitary bees, bumblebees, butterflies and epigeal arthropods) responded negatively to crop yield. With the exception of plants, there were generally low or no diversity gains through organic farming when compared with conventional farming at similar yields. These results indicate that an increase in biodiversity comes about largely through a considerable reduction in yield independent of the farming system. The higher biodiversity levels in organic compared with conventional farming observed in many studies (Bengtsson, Ahnstrom & Weibull 2005; Hole *et al.* 2005) may simply reflect the lower production levels rather than more wildlife-friendly farming methods *per se*. These wildlife benefits accrue in low-yielding conventional farms as much as they do in organic ones, and conversely, they disappear in the most intensive organic farms whose yields rival those of conventional practices.

The shape of the yield vs. biodiversity relationship varied between taxa. Hence, our results indicate that there is no single solution to the debate concerning sparing vs. sharing, suggesting instead that the solution may differ depending on the species group and the productivity of the agricultural landscape. Taxa that require yields to be reduced to very low levels before a biodiversity benefit is realized were typically mobile taxa, such as epigeal arthropods, and flower-visiting insects, such as solitary bees and butterflies (abundance only). These groups typically utilize a range of habitats, using crop fields to some extent as foraging habitat, but most also require undisturbed (semi-)natural habitats as nesting and hibernation sites to fulfil their life cycles. These species groups are often more abundant on organic farms due to their higher floral diversity (Holz-

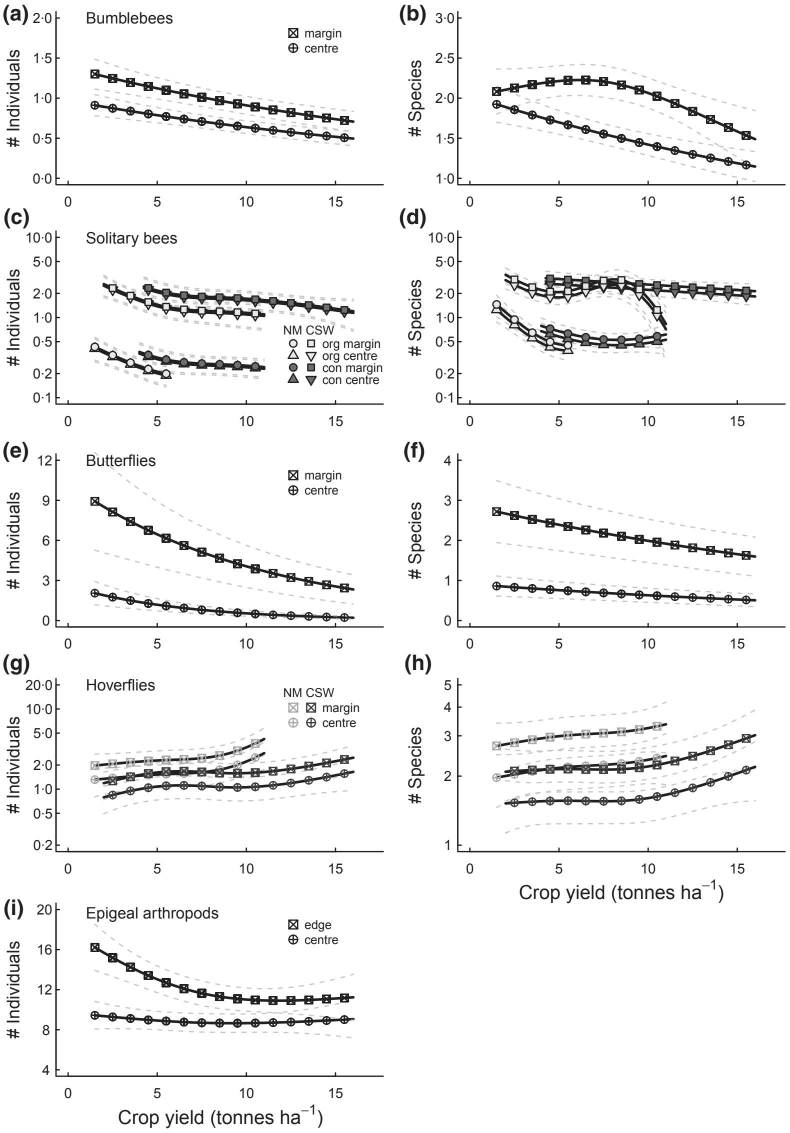

Fig. 2. The relationship between crop yield and the number of individuals and species, respectively, of bumblebees (a + b), solitary bees (c + d), butterflies (e + f) and hoverflies (g + h), and number of epigeal arthropods (i) in crop field centres and edges or margins of organic and conventional crop fields in two regions of England (CSW – Central South West, NM – North Midlands). Dashed grey lines represent range of predicted means ± standard errors. Predictions in c, e and g are for hotspots. The curvature was identical but with lower intercept for solitary bees and hoverflies in coldspots, while there was no relationship with yield for butterflies in coldspots. Note that the number of pollinator individuals is per trap, while the number of pollinator species is per within-field-location (three traps).

schuh *et al.* 2007; Rundlof, Bengtsson & Smith 2008; Gabriel *et al.* 2010), but they can be even more abundant in field margins and nature reserves, such as grasslands of high nature conservation value (Ockinger & Smith 2007; Hodgson *et al.* 2010). For these taxa, our results suggest that effective conservation may require very extensively 'wildlife-friendly' shared land or specifically 'spared' conservation land. This may be (semi-) natural land outside agricultural production and/or uncultivated field margins, such as wildflower strips (Aviron *et al.* 2009), which are managed for biodiversity and also provide nesting habitat (Benton 2012).

For plants, the response curve between species density and crop yield differed between organic and conventional management. While organic and conventional fields exhibited similar plant numbers at high yields, species density increased dramatically with reductions in yield in organic fields leading to much higher densities compared with conventional fields. Therefore, organic farming at average organic yields will produce reasonable biodiversity benefits and can be a particularly beneficial wildlife-friendly method to promote plants within a production system, but if pushed towards intensive levels (i.e. the average conventional yield), it ceases to produce a benefit. All conventional fields were sprayed with herbicides (Table S1, Supporting information), and this most likely underpins the difference in plant species density from organic fields. Recently, Geiger *et al.* (2010) confirmed the overwhelming negative effects of pesticides on various farmland taxa. However, beside pesticide use, this pattern may be linked to other management decisions, such as the amount of nitrogen fertilization and the length of crop rotation, which determine crop yield (Table S1 and Fig. S1, Supporting information). As farmers increase inputs, they increase the density of crops and negatively affect plant diversity, specifically promoting nitrophilous and competitive weeds at the expense of other wild species (Kleijn & vanderVoort 1997). In organic fields, the

Table 2. Averaged predicted farmland biodiversity and percentage change in diversity after the effect of yield has been taken into account

	Centre	Edge/ margin	Percentage change location-within-field	Conventional	Organic	Percentage change farm management	Coldspot	Hotspot	Percentage change landscape-scale management	CSW	NM	Percentage change region
Plants (% cover)[b]	3·7	6·9	85	2·1	8·6	318	5·3	5·3	0	5·3	5·3	0
Plants (species)[c]	4·4	6·7	50	3·4	7·7	124	5·5	5·5	0	5·5	5·5	0
Bumblebees (individuals)[f]	0·7	1·0	43	0·9	0·9	0	0·9	0·9	0	0·9	0·9	0
Bumblebees (species)[g]	1·6	2·2	39	1·9	1·9	0	1·9	1·9	0	1·9	1·9	0
Solitary bees (individuals)[f]	0·8	0·8	5	0·9	0·6	−33	0·7	0·9	34	1·4	0·2	585
Solitary bees (species)[g]	1·3	1·5	16	1·6	1·3	−19	1·4	1·4	0	2·3	0·5	375
Butterflies (individuals)[h]	0·8	5·3	527	3·1	3·1	0	3·1	3·0	−2	3·1	3·1	0
Butterflies (species)[i]	0·7	2·2	216	1·4	1·4	0	1·4	1·4	0	1·4	1·4	0
Hoverflies (individuals)[f]	1·3	1·9	50	1·6	1·6	0	1·4	1·8	27	1·2	2·0	−40
Hoverflies (species)[g]	1·8	2·5	37	2·2	2·2	0	2·1	2·3	8	1·8	2·6	−30
Epigeal arthropods (individuals)[j]	8·8	11·9	36	10·3	10·3	0	10·3	10·3	0	10·3	10·3	0
Average across all taxa			100			35			6			81

Predictions were made for taxa with significant associations with yield and obtained from statistical models in Table S4 (Supporting information) using all combinations of predictor variables: crop yield in a sequence between $^{-1}$ and 11 tonnes ha^{-1} with 0·25 increments, location-within-field, farm management, landscape-scale management and region.

[b–j]See Table 1.

average levels of inputs were much lower than their conventional counterparts (Table S1, Supporting information) and may have promoted plant species density substantially (Kleijn *et al.* 2009). Moreover, in the conventional fields of our study, short crop rotations were associated with greater total nitrogen fertilizer and crop management passes (especially herbicides), larger farms and a reduced number of farm products (Table S2 and Fig. S3, Supporting information). Hence, beside direct field management effects (i.e. increased inputs), a loss of spatial and temporal heterogeneity occurs at farm scales that may itself have direct or indirect impacts on farmland biodiversity (Benton, Vickery & Wilson 2003).

Species density of bumblebees declined in a concave-down shape with increasing crop yield in margins. Bumblebees may be less sensitive to agricultural intensification compared with solitary wild bees and butterflies because they respond to their surroundings at larger spatial scales due to generally larger foraging ranges (Steffan-Dewenter *et al.* 2002; Osborne *et al.* 2008). Moreover, bumblebees most likely enter cereal fields to exploit (non-crop) floral resources of weeds, which themselves displayed a concave-downward response to yield.

Hoverflies were the only species group that responded positively to crop yield. This might be related to their larval food source (Appendix S3, Supporting information). Indeed, if we subdivide hoverfly species into those with aphidophagous, phytophagous and microphagous larvae, we observe a differential response of the hoverfly community to land-use intensity: aphidophagous hoverflies, which are the majority of hoverflies in our study, were positively related to crop yield and conventional farming, while phytophagous and microphagous hoverflies were related to organic farming, where floral resources and organic matter from organic fertilizer (such as manure) are more abundant (Power & Stout 2011).

The organic/conventional yield ratio in our study was lowest in arable-dominated landscapes and highest in mixed landscapes (Appendix S2, Supporting information). de Ponti, Rijk & van Ittersum (2012) showed that organic/conventional wheat yield ratios declined as conventional yields increased, suggesting higher yield gains in conventional compared with organic fields in more productive landscapes or with higher inputs of fertilizer and pesticides. Given these results and the yield vs. biodiversity relationships observed in our study, it is likely that the greatest gains in biodiversity per unit crop yield would occur in mixed and low-productivity landscapes. This result conflicts with the existing consensus that maximal biodiversity gain will occur by promoting organic farms in homogeneous, intensive landscapes (Rundlof & Smith 2006; Holzschuh *et al.* 2007). However, this pervading consensus does not consider the yield differences and the associated additional area of land necessary for food production. In addition, in the UK, organic farming is more prevalent in low-productivity and mixed landscapes (Gabriel *et al.* 2009), which creates 'naturally' aggregated areas that are beneficial to biodiversity (Gabriel *et al.* 2010). In highly productive agricultural landscapes, our results suggest that effective conservation may require specifically 'spared' land, which is managed for wildlife.

Of course, land-sharing and land-sparing approaches are only the ends of a continuum. Land can be 'spared' at very different scales. If sparing is implemented at a coarse scale, spared land would be geographically distinct and very different in character and biodiversity from agricultural land (Phalan *et al.* 2011). In contrast, if sparing is implemented at fine scales, spared land could be on farms (e.g. margins and non-cropped areas) leaving aside field centres for intensive production. Such fine-scale land-sparing approaches, which are conceptually in the transition to wildlife-friendly farming, are likely to support species associated with and living on the managed farmland and may also potentially promote ecosystem services (a function that has been usually associated with wildlife-friendly farming only, see Fischer *et al.* 2008; Tscharntke *et al.* 2012). In a companion study to this one (using the same farms and nearby nature reserves), Hodgson *et al.* (2010) show that the optimal landscape design to manage butterflies depends on the landscape context, with organic farming being more likely to be favoured in mosaic landscapes, while a combination of conventional land with specifically targeted non-farmed conservation areas is more effective in intensive arable landscapes.

When interpreting our results, some aspects should be borne in mind. First, yield and biodiversity are affected by processes at different scales. Yield may depend more on local conditions, that is, the field management, crop variety, soil and local climate, than does biodiversity, which is also affected by larger spatial scale processes, for example, landscape structure (Schweiger *et al.* 2005) and longer temporal scales, for example, land-use history (Lunt & Spooner 2005). Furthermore, the environmental impacts of farming may occur at scales beyond the farm, for example, through nitrogen leaching and greenhouse gas emissions (Ewers *et al.* 2009), and similarly, the biodiversity benefits of organic practice may affect neighbouring farms (Gabriel *et al.* 2010). Additionally, our yield figures do not include the full life cycle economic and environmental costs of inputs, such as fertilizer and pesticides. Hence, we may underestimate the negative impacts of (conventional) farming on local (and indeed global) biodiversity.

Second, apart from birds, diversity was measured at the field scale, and the observed patterns in diversity may change at larger scales. For example, as organic fields have more diverse crop rotations with a smaller proportion of wheat, higher alpha diversity in fields of a different crop and higher beta diversity between fields and farms may lead to higher species numbers at coarse scales (Gabriel *et al.* 2006).

Third, the pairing of farms and landscapes improves statistical comparability, but it usually narrows down the selection and reduces contrasts. The most intensive conventional farms and the most productive arable landscapes are not selected because of the scarcity of organic farms in the most productive landscapes (Rundlof & Smith 2006; Gabriel *et al.* 2009). Hence, the conventional farms in our study may perform better in terms of biodiversity and worse in terms of yield than more typical conventional farms. However, the comparison of diversity at similar yields should not be influenced by this selection.

Finally, our study examines only a single crop type, winter cereals (predominantly winter wheat). While this is the most important arable crop in Europe, it is far from being the only one. Absolute yields and differences between organic and conventional yields vary between different crops, between crops and animal products and between different landscapes and regions (de Ponti, Rijk & van Ittersum 2012; Seufert, Ramankutty & Foley 2012). Seufert, Ramankutty & Foley (2012) report organic yields to be 34% lower when farming systems are most comparable. Our figures show more pronounced differences than this (54% lower), although we used farms that were matched for enterprize type, soil and location and thus accounted for potential biases due to the farm and landscape types that organic farms occur in other studies (Gabriel *et al.* 2009; Norton *et al.* 2009). However, farm management decisions are generally made on the basis of profitability rather than yield *per se*, and the higher market price of organic produce and lower input costs may compensate farmers for the lower yields, allowing enhanced biodiversity while maintaining profitability (Sutherland *et al.* 2012). Alternatively, organic yields might be even smaller if we accounted for non-food crops, that is, green manure crops, within the crop rotation. Therefore, it is difficult to predict how much more land is needed to produce the same amount of food with organic agriculture, but it seems clear that it requires substantially more land (Goklany 2002; Trewavas 2004). Whole-farm approaches or indeed whole economy approaches are required, where biodiversity and yields at larger spatial and temporal scales should be compared.

Conclusions

In summary, farmland biodiversity is typically negatively related to crop yield; generally, organic farming *per se* does not have an effect other than via reducing yields and therefore increasing biodiversity. Only plants benefited substantially from organic farming at comparable yields. It is not clear that the relatively modest biodiversity gains can be justified by the substantial reductions in food production. Indeed, the relatively low yields of organic farms may result in larger areas of land being brought into agricultural production (locally or elsewhere), at a biodiversity cost much greater than the on-farm benefit of organic practice (Goklany 2002; Hodgson *et al.* 2010). Thus, organic farming should be mainly encouraged in mosaic (low productivity) landscapes, where yield differences between organic and conventional agriculture are lower. The concentration of organic farms into hotspots with high fractions of organic land could provide additional biodiversity benefits. In high-productivity landscapes, organic farming is not an efficient way of maximizing biodiversity and yield, but land sparing might be. However, land sparing cannot be left to chance as landscapes with high productivity and high profit margins stimulate productivity, which ultimately inhibits conservation efforts (Ewers *et al.* 2009). If ecosystem services need to be maintained, land sparing at fine scales in the form of specifically managed margins or nature reserves will need to be integrated into planning and incentive schemes for landscapes where intensive agriculture dominates.

Acknowledgements

We thank the farmers, the field and laboratory assistants and the RELU SCALE team for collaboration, J. Hodgson for the 2008 butterfly data, U. Schmutz for farm economics data and R. Morris, F. Burger and A. Dietzsch for pollinator ID. Thanks to Janne Bengtsson and one anonymous referee for their critical and helpful comments. The research was funded as part of the UK Research Councils' Rural Economy and Land Use Programme (RELU) (RES-227-25-0006). D.G. was supported by the British Ecological Society and the UKPopNet.

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Received 30 July 2012; accepted 28 November 2012
Handling Editor: Ingolf Steffan-Dewenter

Supporting Information

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

Appendix S1. Biodiversity surveys.

Appendix S2. The field, farm and landscape management of organic and conventional farms.

Appendix S3. Aphidophagous hoverflies are positively related to crop yield, but not non-aphidophagous hoverflies.

Fig. S1. The relationship between crop yield and field, farm and landscape measures in conventional fields.

Fig. S2. The relationship between crop yield and field, farm and landscape measures in organic fields.

Fig. S3. The relationship between length of crop rotation and the amount of synthetic nitrogen fertilizer, the number of crop protection applications, the number of different crops in rotation, the number of herbicide applications, farm size, livestock units per grazed land and the number of farm enterprises in conventional fields.

Fig. S4. The relationship between species density and abundance for all investigated taxa.

Table S1. Summary statistics describing indicators of field, farm and landscape management on 96 conventional and 69 organic winter cereal fields.

Table S2. Correlation matrix of field, farm and landscape measures in conventional winter cereal fields.

Table S3. Correlation matrix of field, farm and landscape measures in organic winter cereal fields.

Table S4. Summary statistics of best models.

Table S5. Predicted abundance and species density of farmland biodiversity.