

LETTER

Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control?

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Abstract

While many studies have demonstrated that organic farms support greater levels of biodiversity, it is not known whether this translates into better provision of ecosystem services. Here we use a food-web approach to analyse the community structure and function at the whole-farm scale. Quantitative food webs from 10 replicate pairs of organic and conventional farms showed that organic farms have significantly more species at three trophic levels (plant, herbivore and parasitoid) and significantly different network structure. Herbivores on organic farms were attacked by more parasitoid species on organic farms than on conventional farms. However, differences in network structure did not translate into differences in robustness to simulated species loss and we found no difference in percentage parasitism (natural pest control) across a variety of host species. Furthermore, a manipulative field experiment demonstrated that the higher species richness of parasitoids on the organic farms did not increase mortality of a novel herbivore used to bioassay ecosystem service. The explanation for these differences is likely to include inherent differences in management strategies and landscape structure between the two farming systems.

Keywords

Agro-ecology, biodiversity, networks, parasitoid diversity, species interactions.

INTRODUCTION

The extent to which biodiversity can be lost before it affects the provision of ecosystem services is unclear. Services such as natural pest control are the result of the complex network of interactions among species in a community. These services provide substantial, if not invaluable economic benefits to humans particularly in food production (Losey & Vaughan 2006; Klein *et al.* 2007). Many studies suggest that

a large pool of species is necessary to maintain the functioning of ecosystems, especially in intensive agricultural landscapes (Loreau *et al.* 2001; Tschardtke *et al.* 2005). For example, for insect pollinators, maintaining a diversity of species is essential for sustaining plant pollination services because of yearly variations in community composition (Kremen *et al.* 2002). For the service of natural pest control the situation is more complex. Snyder *et al.* (2006) found that a greater number of predator species increased

aphid suppression, but in contrast Rodriguez & Hawkins (2000) found that species-rich parasitoid communities did not result in higher parasitism rates than species-poor communities. Rather it seems that at least in some host-parasitoid communities, one or a few species drive the dynamics of the system with additional species contributing little to pest control (Hawkins 1994).

Governments worldwide are investing heavily in schemes that aim to reverse the trend of declining biodiversity in intensive agricultural landscapes (Benton *et al.* 2002; Carvell *et al.* 2007; Whittingham 2007). Wide-scale conversion to organic farming has been suggested as one means for reversing the process of agricultural intensification, and is thought to lead to increased diversity of up to 30% for some taxa (Bengtsson *et al.* 2005; Hole *et al.* 2005). Organic farms generally have specific crop rotations, greater areas of semi-natural vegetation (Gibson *et al.* 2007) and do not use synthetic pesticides (Lampkin 1999). Pest control on organic farms relies largely on cultural practices and naturally occurring predators and parasitoids to control insect pest outbreaks. If organic farms support higher levels of biodiversity, they may be better protected against the effects of invasion by alien species (including novel pest species) through biotic resistance. There is evidence that as species richness increases, resistance to invasion increases (Kennedy *et al.* 2002). Consequently organic farms that have higher biodiversity (in the form of more species of predators, parasitoids and pathogens) may be better protected against novel pests in comparison with their conventional counterparts. However, ecological theory indicates that organic farms may be more vulnerable to extinction cascades. Connectance is a measure of network complexity and is calculated as the number of realized links divided by all potential links in the network. General relationships between connectance and the number of species in a network are still unclear (Martinez 1993; Murtaugh & Kollath 1997). However, Dunne *et al.* (2002) demonstrated that in ecological networks, robustness to simulated species loss increases with network connectance. Networks with high connectance seem to delay the onset of the threshold past, which they display extreme sensitivity to the removal of species (Dunne *et al.* 2002). In general, as insect-dominated networks become more species rich (assuming a similar composition of generalist to specialist consumers), connectance decreases in an exponential curve (Schoenly *et al.* 1991), suggesting that organic farms that support greater levels of biodiversity may be less robust to species loss in comparison to their conventional counterparts.

Traditionally descriptors such as species richness, species abundance and diversity indices have been used to assess the anthropogenic impact on natural communities. However, these descriptors may fail to detect important

changes to community structure, species interactions and ecosystem function (Tylianakis *et al.* 2007). Furthermore, these descriptors tell us little about the functioning of an ecosystem or the provision of essential services (Kremen 2005; Tschamtkke *et al.* 2005). Ecological networks such as food webs provide a powerful tool for examining complex communities of species that interact across trophic levels and are essential for revealing the functional components of biodiversity (McCann 2007). Here, our aim is to use a food-web approach to characterize both community structure and function on replicate organic and conventional farms, with networks described at the scale of entire farms. Biodiversity studies in agro-ecosystems have usually been carried out at the field scale (e.g. Pocock & Jennings 2008; Firbank *et al.* 2003). However, such field-scale comparisons may be inappropriate if there are emergent properties at the whole-farm scale (Vandermeer 1997). Quantifying the interactions between species at the community level is a unique approach and reflects our aim to study the community function as well as community structure. Our objectives are fourfold: (1) to use food webs from replicated farms to determine whether organic farms are more species rich than conventional farms at three trophic levels sampled at the scale of whole farms. Given that previous studies have demonstrated that organic farms support greater levels of biodiversity (Bengtsson *et al.* 2005; Hole *et al.* 2005), we predict that our organic farms will have higher species richness at all three trophic levels in comparison with our conventional farms. (2) To determine whether the two farming systems have a different network structure. Here our predictions are twofold: first, that as a consequence of their higher species richness, the organic farms will have lower connectance than conventional farms; second, given that organic farms are expected to provide greater levels of natural pest control, we predict that more parasitoid species will attack each herbivore species. (3) To use a field experiment to test whether organic farms provide a more effective ecosystem service of natural pest control. We predict that the higher species richness of parasitoids on the organic farms provides biotic resistance (e.g. Kennedy *et al.* 2002) to the invasion of alien herbivores and thereby the establishment of novel pests. (4) To test the robustness of organic and conventional farms to species loss. Here we predict that the lower connectance on the organic farms will lead to the networks being less robust to species loss (Dunne *et al.* 2002).

MATERIALS AND METHODS

Ten pairs of organic and conventional farms were chosen in south-west England. Organic farms had been certified as organic for an average of 7.3 years (range 3–12 years) at the

start of the study. All were mixed farms, with arable crops, pasture and livestock and had similar soil types. Organic farms were selected first, then paired with a non-adjointing conventional farm of similar size within 5 km (Gibson *et al.* 2007; Table S1). All other features of the farms such as the location and proportion of semi-natural vegetation patches, arable crop types, and management strategies within areas were not controlled for, as these are considered inherent differences between organic and conventional farming systems that we wished to incorporate into our study.

Prediction 1. Organic farms have higher species richness at all three trophic levels

All farms were mapped and the area occupied by each habitat-type (referred to as landscape elements here) calculated. Landscape elements comprised pasture fields, arable fields (a variety of crop types), hedgerows, woodlands, field margins, rough ground (areas not used for primary production), set-aside, game cover, vegetable growing areas and orchards (Gibson *et al.* 2007). Each landscape element was sampled according to the area it occupied on the farm. Proportionately more effort went into sampling larger elements, as a large area of a low-diversity landscape element may contribute more species than a small area of a high-diversity landscape element. For example on one of the farms, in 2005, the 150-m² transect was split up into 50 m² of grass field, 35 m² of a second grass field, 18 m² of an arable field (barley), 21 m² of arable (wheat), 9 m² of arable (oats), 11 m² of woodland, 1 m² of rough ground, 4 m² of hedgerow and 1 m² of field margins. In 2005, a total transect area of 150 × 1 m was sampled on each farm for both plants and herbivores on six occasions (April–September) and all landscape elements were sampled per visit. In 2006, a subset of landscape elements was sampled (arable fields, woodlands and hedgerows) and a total transect area of 100 × 1 m was sampled per farm on five occasions (May–September). Different patches of landscape element were used in each survey, unless the landscape element was rare, in which case repeated surveys had to be within the same patch. Within each patch, the transect location was varied so that no area was sampled more than once.

In each transect, we recorded plant diversity and abundance in the field and collected herbivores for rearing in the laboratory. Plants were identified to species (or genus if this was not possible) and given an abundance measure of 1–4. Category 1 plants were rare, only present once to a few times in the whole transect, category 2 were present in high enough numbers to be seen easily (occupied < 10% of the transect area), category 3 could be seen throughout the whole transect (< 50% of the area) and category 4 were the most abundant (> 50% of the area). All vegetation (shorter

than *c.* 2.5 m) was visually inspected, sweep netted, and if tall enough, beaten over a beating tray and all leaf-mining Diptera, leaf-mining Lepidoptera and externally feeding Lepidoptera (i.e. semi-concealed and free living) were collected. The herbivores were reared individually under ambient conditions in a laboratory until either an adult herbivore or parasitoid emerged. Each herbivore was checked every 2–3 days and food (fresh host plants collected from the field) and moisture (on a cotton roll) was added as necessary. Once the herbivore had pupated, all food and moisture were removed from the container. For those Lepidopteran species that pupate, underground fresh soil was added to the container. Leaf-mine appearance, herbivore morphology and host plant species were used to identify herbivores. All dipteran leaf-miners and parasitoids, plus a subset of adult lepidopterans, were identified by specialist taxonomists (see Acknowledgements). The plant on which an herbivore was found was recorded as the most likely feeding host. Insects not identified to genus or morphospecies were excluded from the data set, this amounting to only 76 individuals from 16 909 rearings.

Rearing data from both years were combined to construct 20 whole-farm food webs. Multiple parasitoids emerging from a single host were represented as a single rearing record. Only two hyper-parasitoid species were collected (both in low abundance) and these were included in the third trophic level as we could not accurately identify their parasitoid host (Lewis *et al.* 2002). The number of species collected on each trophic level per farm along with a series of qualitative and quantitative network indices (see Prediction 2) were analysed in GenStat using a paired (or repeated measures) multivariate analysis of variance (MANOVA) (Gibson *et al.* 2007), with farming system as a treatment factor. We had multiple dependent variables that we wished to analyse, and if we had used multiple one-way ANOVAs, we would have raised the probability of a Type I error. MANOVA controls the experiment-wide error rate. The alpha values for the subsequent univariate tests were Bonferroni corrected. However, adjusting these outputs further increases the likelihood of inflating Type II errors, particularly for ecological studies such as ours which typically involve high variability. Moran (2003) indicates that ecologists should not be constrained by correcting for multiple testing. Throughout this manuscript for completeness and transparency, we present both adjusted and non-adjusted alpha values ($\alpha = 0.05$), but focus our discussion on results prior to adjustments. The number of species in each trophic level was log₁₀-transformed, and C_r arcsin-transformed. The residuals were checked and were approximately normally distributed, and the variances and covariances were roughly homogeneous.

The parasitism rate (percentage) per farm was calculated for lepidopteran and dipteran hosts separately

using live rearings only. Rearings from which no host or parasitoid emerged were removed from the data set.

Prediction 2. Organic and conventional farms have a different network structure

Partial Mantel tests were used to test whether there was a difference in the overall network structure between the two farming systems. This test asks if there is a relationship between two matrices whilst holding a third matrix constant. The first matrix was calculated using the quantitative Bray Curtis dissimilarity index (also known as Sorensen quantitative index) between species interaction frequencies. The two independent hypothesis matrices were; System: farms with the same farming system, e.g. organic and organic, were given a one and all other combinations a zero; and Pair: each experimental pair of farms in the same geographical location were represented by one, and all others with a zero. A mantel statistic (r) was calculated to measure the relationship between the first two matrices whilst controlling for the third, and Monte Carlo randomization was used to test the null hypothesis that there was no relationship between the matrices using the program Zt version 1.1 (Bonnet & Van de Peer 2002). We tested whether there was a significant relationship between the differences in species interaction frequencies and farming system (System) when controlling for the effect of geographic pairing (Pair). Then the matrices were reversed (Pair, with System held constant) to test whether there was a relationship between differences in species interaction frequencies and geographic pairing when farming system is held constant. This analysis was repeated after removing rare interactions (interaction frequency = 1) to determine whether the rare interactions were influencing the effect of farming system on network structure.

Quantitative (C_{qherb} , C_{qpara}) and qualitative measures of connectance (C_r) were calculated per farm, the latter for comparison to the robustness analyses of Dunne *et al.* (2002). (C_r) was calculated as the number of realized links (I_r) divided by the number of potentially possible links (I_{max}) (Thompson & Townsend 2003; Lafferty *et al.* 2006). Quantitative connectance for both the plant to herbivore (C_{qherb}) and herbivore to parasitoid level (C_{qpara}) was calculated according to Bersier *et al.* (2002) and Tylianakis *et al.* (2007). Vulnerability is the mean number of parasitoid species attacking each host species. We calculated the standard qualitative vulnerability (V) along with the quantitative, weighted equivalent of vulnerability (V_q) at the herbivore to parasitoid level (Bersier *et al.* 2002) that includes information on the interaction strength of each link. These indices were analysed in GenStat using a paired

MANOVA, with farming system as a treatment factor (for further details see Prediction 1).

Prediction 3. Organic farms are more resistant to the establishment of novel pests through greater levels of natural pest control

The underlying rationale of this experiment was to introduce a novel pest to determine the effectiveness of natural pest control on the two farms. Clearly it would have been unethical to release a genuine pest species, therefore we used a surrogate pest in the form of an alien leaf-miner *Phyllonorycter leucographella* (Lepidoptera: Gracillariidae) that is already present in the UK. Other leaf-miners such as *Liriomyza* spp. (vegetable leaf-miners), *Chromatomyia syngenesiae* (chrysanthemum leaf-miner) and *Phyllonorycter crataegella* (apple blotch leaf-miner) are significant agricultural pests around the world. Thus whilst *P. leucographella* is not currently pestiferous, it provided a realistic model for testing the resistance of the farms to the establishment of a novel species. This leaf-miner was chosen as it would not be naturally present on the farms (and therefore would be completely novel to the parasitoid community) as it is specific to the non-native shrub *Pyracantha coccinea*, which is only found in urban areas. Moreover, it is already known that *P. leucographella* is attacked by numerous native parasitoids in the UK (Godfray *et al.* 1995; Nash *et al.* 1995; Rott & Godfray 2000), making it a good species with which to bioassay the local parasitoid communities on the 20 farms.

Fifty *Pyracantha* bushes were planted in a single, centrally located plot, away from woodland and along a hedgerow, on each farm in late 2004. Within paired farms, the planting positions were matched. During summer 2005/2006, immature *P. leucographella* were introduced to the field plots via inoculated potted plants, which had been kept in parasitoid-free conditions. Each farm within a pair received the same number of inoculated potted plants with approximately the same number of visible mines. In the spring and summer of 2007, each plot was sampled for late instar leaf-miners, as early instars have a very low rearing success. A total of 2252 leaf-miners were reared successfully from 18 farms (one of the pairs was excluded due to low miner numbers). All parasitoids were then identified by taxonomists.

The number of parasitoid species (\log_{10} -transformed), and proportion parasitism (arcsin-transformed) were analysed using a paired MANOVA in GenStat. The number of live rearings per plot were analysed using a nonparametric paired t -test (Wilcoxon signed-rank test). The percentage parasitism in the whole-farm networks was compared between organic and conventional farms using a nonparametric paired t -test (Wilcoxon signed-rank test).

Prediction 4. Organic farms have a higher robustness to species loss

The robustness of the networks to simulated species loss was tested by calculating a ‘robustness’ measure for each network using the methods of Dunne *et al.* (2002). For each farm network, we systematically removed species, then calculated the total species loss (i.e. primary species removals plus secondary extinctions). We simulated species loss using three scenarios: random species removal, least connected species removed first and most connected species removed first. The robustness measure tells us what fraction of species needs to be removed as primary extinctions to result in a total loss of 50% or more species. The maximum possible robustness is 0.50 and minimum is $1/S$, where S is

the number of species (Dunne *et al.* 2002). The measure of robustness was compared between organic and conventional farms using nonparametric paired *t*-tests (Wilcoxon signed-rank test) in SPSS (SPSS Inc., Chicago, IL, USA).

RESULTS

The 20 food webs contained 374 plant, 370 herbivore and 193 parasitoid species, linked together in complex networks each containing 143–274 species (Fig. 1). Pest species such as *Pieris brassicae* (large white butterfly), *Pieris rapae* (small white butterfly), *Plutella xylostella* (diamond-back moth), *Epiphyas postvittana* (light-brown apple moth), *Mamestra brassicae* (cabbage moth), *Lyonetia clerkella* (apple leaf-miner) and *Scaptomyza flava* (drosophilid leaf-miner) were present in

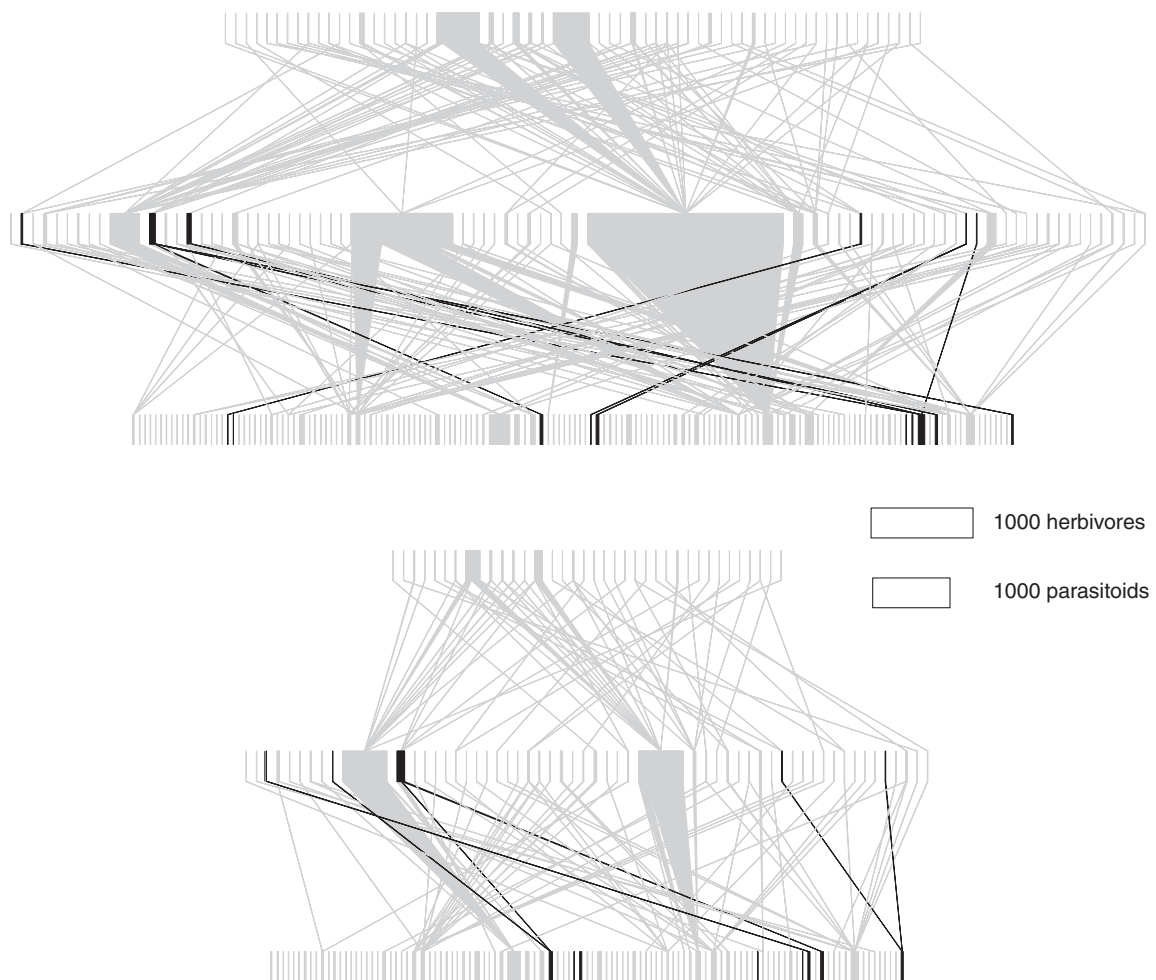


Figure 1 One of the 10 pairs of farm networks. The bottom level of each web shows all the plant species sampled on the farm, the middle level the insect herbivores and the top level the parasitoids. Each bar indicates a different species, and for herbivores and parasitoids the width of the bars represents their abundance on the farm; plants were given an abundance measure on a scale of 1–4. The lines between trophic levels indicate that these two species are interacting and the width of the lines indicates the frequency of this interaction. Arable plant species and their herbivores have been shaded black.

the farm networks. The percentage of successful rearings across all herbivore groups was 49%, similar to that of Henneman and Memmott (2001) and there was no difference between farming systems in the proportion of unsuccessful rearings per farm (Wilcoxon signed-rank test: lepidopterans $Z = -1.478$, $P = 0.139$; dipterans $Z = -1.070$, $P = 0.285$).

Prediction 1. Organic farms have higher species richness at all three trophic levels

As predicted, organic farms had significantly greater numbers of plant ($F_{1,9} = 7.87$, $P = 0.021$), herbivore ($F_{1,9} = 21.10$, $P = 0.001$) and parasitoid ($F_{1,9} = 7.16$, $P = 0.025$) species than their conventional counterparts (Fig. 2).

Prediction 2. Organic and conventional farms have a different network structure

The partial mantel tests revealed that network topology was different between the two farming systems. Thus there was a significant relationship between species interaction frequencies and farming system when controlling for the effect of geographical pairing ($r = -0.1806$, $P = 0.017$). When the independent matrices were reversed (pair first, then system), we found no significant relationship between geographical pairing and species interaction frequencies when farming system was held constant ($r = -0.0725$, $P = 0.126$), indicating that the differences in species interaction frequencies are more strongly determined by farming system than the geographic location of the farms. This analysis was repeated after rare interactions had been removed from the data set, with the same outcome (System first, then Pair: $r = -0.1803$, $P = 0.017$; Pair first, then System: $r = -0.0733$, $P = 0.125$).

As predicted, the increased number of species on organic farms resulted in significantly lower connectance values on organic farms (C_r : $F_{1,9} = 4.97$, $P = 0.049$, organic median $C_r = 0.012$, conventional median $C_r = 0.014$). However, this result should be treated with caution as the P -value was marginal and the quantitative connectance indices were non-significant (plant–herbivore level: $F_{1,9} = 1.26$, $P = 0.290$, organic median $C_{qherb} = 0.017$, conventional median $C_{qherb} = 0.019$; herbivore–parasitoid level: $F_{1,9} = 0.99$, $P = 0.346$, organic median $C_{qpara} = 0.049$, conventional median $C_{qpara} = 0.050$). There was also a significant difference in herbivore vulnerability (i.e. the number of parasitoid species attacking each herbivore species) between the farming systems for the quantitative index (weighted vulnerability V_q : $F_{1,9} = 10.15$, $P = 0.011$), although not for its qualitative equivalent (vulnerability V : $F_{1,9} = 1.33$, $P = 0.279$).

In relation to both Predictions 1 and 2, it is worth noting that while use of Bonferroni correction leads to the loss of significance for all but the number of herbivore species, the

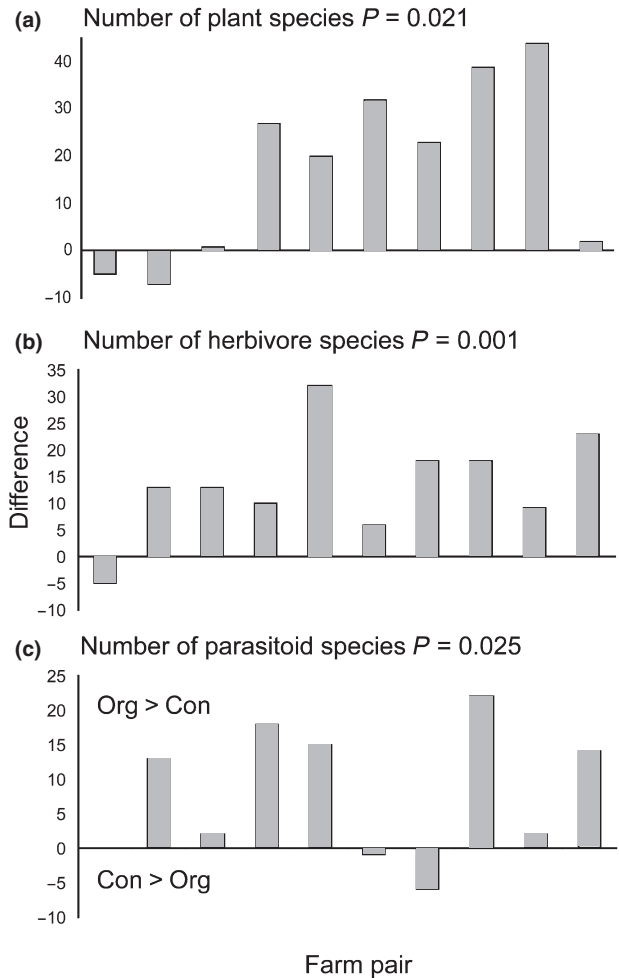


Figure 2 Paired difference between organic and conventional farms: (a) the total number of plant species per farm, (b) insect herbivore species and (c) parasitoid wasp species collected on the farms. Positive figures show more species on organic farms, negative figures more species on conventional farms. Data were analysed using a paired MANOVA in GenStat with farming system as the treatment factor (multivariate tests Wilk's lambda = 0.188, $P = 0.330$). Adjusted univariate test $\alpha = 0.00625$.

probability of finding at least five significant results out of the eight tests prior to correction by chance alone is 0.000125 (calculated as a Binomial expansion).

Prediction 3. Organic farms are more resistant to the establishment of novel pests through greater levels of natural pest control

Phyllonorycter leucographella successfully colonized the 20 *Pyracantha* plots (mean 140 ± 17 live mines per farm). Contrary to our prediction though, there was no significant difference in either the number of parasitoid species attacking *P. leucographella* in the experimental plots or the

Table 1 Novel host experiment (a) showing parasitism of a novel leaf miner host *Phyllonorycter leucographella* on the plant *Pyracantha coccinea*, one pair of farms was removed due to low miner abundance, and the *a posteriori* analysis (b) of the farm networks (see Discussion) involved calculating the number of parasitoid species known to attack *P. leucographella* in the UK that were present on each farm. Similarly the number of parasitoid species recorded attacking each herbivore family per farm was also calculated. Of the 30 herbivore families recorded, 12 families were sufficiently abundant for analysis, and the results from four families are shown in the table. Data were analysed using two separate paired MANOVA in GenStat with farming system as the treatment factor. The adjusted alpha is shown at the bottom of the table. Bold figures are significant at $\alpha = 0.05$.

	Range organic	Range conventional	$F_{1,8}$	P
(a) Multivariate tests Wilk's lambda = 0.697, $P = 0.282$				
Number of parasitoid species attacking <i>Phyllonorycter leucographella</i> reared from each experimental plot (9 farm pairs)	1–4 species	2–6 species	0.91	0.369
Percentage parasitism of <i>P. leucographella</i> in each plot (9 farm pairs)	4.3–46.9%	17.4–62.5%	3.15	0.114
			$F_{1,9}$	
(b) Multivariate tests Wilk's lambda = 1.175, $P = 0.144$				
Number of parasitoids of Gracillariidae species from farm networks (capable of attacking <i>P. leucographella</i>)	1–9 species	3–6 species	1.09	0.324
Parasitoids of Agromyzidae species	0–30 species	0–23 species	6.10	0.036
Parasitoids of Choreutidae species	0–4 species	0–1 species	7.09	0.026
Parasitoids of Noctuidae species	0–3 species	0–1 species	3.86	0.081
Parasitoids of Geometridae species	0–4 species	0–2 species	5.36	0.046

Adjusted univariate test: (a) $\alpha = 0.025$ and (b) $\alpha = 0.01$.

Probability of obtaining at least three significant results by chance out of five is 0.00116.

parasitism rate on the two types of farm (Table 1a). A total of 13 parasitoid species were reared from the plots and percentage parasitism ranged from 4% to 62% (Table 1a). The three most abundant species in the organic plots were the same species in the conventional plots. There was no difference in the number of successful rearings between farming systems ($Z = -0.153$, $P = 0.878$). Looking beyond the specific novel herbivore and using data from the 20 farm networks, there was no difference in the parasitism rates across a range of hosts on organic and conventional farms (parasitism rate lepidopteran hosts: $Z = -1.071$, $P = 0.284$; dipteran hosts: $Z = -1.682$, $P = 0.093$).

Prediction 4. Organic farms have a higher robustness to species loss

We found no difference in robustness (Dunne *et al.* 2002) between organic and conventional networks under any of the three scenarios (random: $Z = -0.510$, $P = 0.610$; least connected: $Z = -1.580$, $P = 0.114$; most connected: $Z = -0.663$, $P = 0.508$). Networks were moderately sensitive to the loss of least connected species first, with 32–43% of primary removals required before a total species loss of 50% was reached. As expected, robustness was much lower when removing most connected species first (9–18% of primary removals). When species were removed at random, 27–32% of primary removals was required.

DISCUSSION

There were significantly greater levels of biodiversity on organic farms in both species richness and species interactions, leading to significant structural differences between organic and conventional food webs. Functional changes between the two farming systems were less apparent. Thus, organic farms did not exhibit better natural pest control than their conventional counterparts, nor were there any differences in robustness to species loss between the two farming systems. In this section, we first discuss the results in the context of our four predictions, and finish by considering the potential uses of ecological networks in agro-ecology.

Prediction 1. Organic farms have higher species richness at all three trophic levels and altered network structure

We demonstrated significantly greater levels of biodiversity on organic farms in terms of species richness at the three trophic levels. While many previous studies have indicated increased species richness and abundance of certain taxa on organic farms (e.g. Feber *et al.* 1997; Wickramasinghe *et al.* 2003), some other studies are inconclusive (Hole *et al.* 2005). This ambiguity probably stems from comparing individual organic to individual conventional fields (Bengtsson *et al.* 2005; Hole *et al.* 2005). Our study, at the whole-farm scale, clearly demonstrates that there are

greater levels of plant, herbivore and parasitoid diversity on organic farms.

The observed increase in biodiversity may result from a range of several factors that are different between organic and conventional farming systems, such as farm structure, pesticide regimes, rotations, historical removal of particular landscape elements and differing management strategies. For the results presented here, the different relative amounts of each landscape element, different management techniques within each landscape element and a combination of both these factors seem to be important. As sampling effort was proportional to the area occupied by each landscape element, the greater diversity at the whole-farm level may be partially related to the greater area of high-diversity landscape elements (such as woodlands) on organic farms. For other landscape elements, area may not be as important as the management techniques within the element. For example, arable fields that take up less area on organic farms (Gibson *et al.* 2007) show greater plant diversity probably in response to weed control tactics, and cropping practices. Clearly both these factors are relevant when considering how whole-farm conversion to organic will influence diversity in agroecosystems. Landscape-level factors have been shown to have an impact on the relationship between diversity and organic farming (Schmidt *et al.* 2005). All 20 farms here were embedded in a complex landscape and a similar study conducted in a more homogenous landscape may find greater differences and/or altered community structure.

Prediction 2. Organic and conventional farms have a different network structure

The results of the partial Mantel tests showed that there are significant structural differences between food webs on organic and conventional farms. There were significant differences in connectance (C_v) and quantitative-weighted vulnerability (V_q), which provide further support for structural differences in networks between the farming systems.

Prediction 3. Organic farms are more resistant to the establishment of novel pests through greater levels of natural pest control

Contrary to expectation, we found no difference in natural pest control between the two farming systems. There was no difference between the farming systems in the number of parasitoid species recruiting to a novel herbivore; furthermore, there was no difference in overall parasitism rate in the whole-farm networks. To explore this result further, we used an *a posteriori* approach to calculate how many parasitoid species known to attack our introduced species were present in each farm's network. These species were identified using Godfray *et al.* (1995), Nash *et al.* (1995) and

Rott & Godfray (2000), in addition to our own rearing records. Although there were clearly more parasitoid species on organic farms (Fig. 2), this approach revealed that we should not expect to see a difference between farming systems in the number of parasitoid species attacking *P. leucographella* in the field experiment (Table 1b). Continuing with this approach for each of the 30 herbivore families on the farms, we predict that if an alien or pest species in the Agromyzidae (Diptera), Geometridae or Choreutidae (Lepidoptera) family were to invade, they would be attacked by more parasitoid species on organic farms, and if members of the Noctuidae family invaded, they may be attacked by slightly more species on organic farms, although this result was marginal (Table 1b).

Prediction 4. Organic farms have a higher robustness to species loss

The increased species richness on organic farms did lead to lower levels of qualitative connectance on organic farms. However, this decrease in connectance did not translate into a difference in robustness to simulated species loss. While Dunne *et al.* (2002) found a clear positive relationship between connectance and robustness, their connectance values vary across an order of magnitude. In contrast, ours, both organic and conventional values, all fall on the lower end of Dunne's scale. Thus the small difference in connectance between farming systems was probably insufficient to affect network robustness (Forup *et al.* 2008). The low threshold for robustness (9–18% for the removal of the most connected species first scenario) suggests that the farm networks (regardless of farming system) may be vulnerable to secondary extinctions and extinction cascades after the loss of relatively few species.

Both organic and conventional farms in south-west England tend to be small in size, mixed and diverse in terms of semi-natural habitat such as woodlands and hedgerows (Defra 2005). Therefore, the minimal functional differences we found between the two farming systems may result from landscape-level factors associated with the study location. More generally, while organic farmers cannot use synthetic pesticides to control weeds and insect pests, there are pesticides (e.g. Rotenone) that have been approved for use by organic farmers and may have equally detrimental effects on the environment as their conventional counterparts (Trewavas 2001). Moreover, conventional farmers are increasingly using more environmentally sensitive management practices (e.g. integrated pest management) rather than relying on routine applications of synthetic pesticides (Lawson 1994). Consequently, the difference between the two farming systems may not be as great as is often assumed and may confound the long held belief that organic farming is 'better' for the environment than conventional farming

(Kirchmann & Thorvaldsson 2000). In more intensively farmed areas (e.g. south-east England), differences in functional aspects between farming systems may be more apparent. However, our organic farms are not unrepresentative as the south-west currently has the highest number of organic farms in the UK (Defra 2005).

Whilst food webs are a convenient means of simultaneously sampling species at multiple trophic levels, like all sampling methods they have limitations. First, food webs contain no dynamic information; rather they are a snapshot of the community over a particular time period, here 2 years. While we rely on the food webs as community descriptors, our field experiment effectively assays the dynamics of the communities. Second, we have only sampled a limited species pool and there are other taxa that are functionally important that were not included in this study and may respond differently to organic farm management. However, food chains comprising plants, insect herbivores and parasitoids include over half of all known species of metazoa (Strong *et al.* 1984), thus our webs will characterize a substantial fraction of biodiversity on farms.

CONCLUSION

The intensification of arable agriculture over the last 50 years has been associated with substantial losses of biodiversity (Tilman *et al.* 2002), and there is considerable concern that intensive agriculture is not compatible with the conservation of biodiversity (Robinson & Sutherland 2002). Organic farming is often thought of as the panacea for the problems associated with biodiversity conservation in intensive agricultural landscapes. Our study shows that there are greater levels of biodiversity on organic farms and this translated into altered food-web structure, even when compared to conventional farms located in a complex landscape. Functional differences were less clear though as our experiment demonstrated that our novel herbivore was not attacked by more species of parasitoid, a result supported by the background parasitism levels in the 20 networks. However, we could predict that novel herbivores in three other families would be attacked by more species of parasitoids on organic farms. A priority for future research is determining what network structural changes mean for ecosystem function and the sustainability of agricultural landscapes (McCann 2007). To date, information on declines in biodiversity is clustered around particular taxa (e.g. farmland birds, mammals, arable weeds). However, the distribution and abundance of these groups may not provide the data needed for the sustainable management of agriculture. Rather, a better understanding of how species interact within a community and how communities function at the landscape scale could be keys to the maintenance and utilization of biodiversity in agroecosystems.

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