Supplementary information

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Ecological networks reveal resilience of agro-ecosystems to changes in farming management

Supplementary Methods 1 | The Farm Scale Evaluations (FSEs).

Towards the end of the 1990s, there were several Genetically Modified, herbicide-tolerant (GMHT) crops that were close to commercial use in Europe. There were concerns raised that the adoption of these crops, which would entail changes to the management of broad-spectrum herbicides, would further contribute to the declines in farmland biodiversity experienced since the 1960s. Consequently, the UK Government established the Farm Scale Evaluations as a trial to test whether four of these GMHT crops, spring sown beet (*Beta vulgaris*), maize (*Zea mays*) and oilseed rape (*Brassica napus*) and winter-sown oilseed rape (*B. napus*), would affect the farmland biodiversity of Great Britain. The trial was to be run by a consortium of scientists under the guidance of an independent Scientific Steering Committee between 2000 and 2005.

The overarching null hypothesis for the FSEs was that "there was no effect of the herbicide management of GMHT crops on biodiversity", but with the expectation that effects on biodiversity would be mediated by the direct effects killing of the weed component of diversity through herbicide use and indirect effects on wider biodiversity through the loss of refuge and food resources provided by these weeds. The FSE scientists and steering committee agreed that a significant effect on any taxon was a change in amount (count, density, biomass) of 50%, either up or down. They also agreed a set of protocols designed to collect as wide a sample of the plant and invertebrate biodiversity in an around fields where the GMHT crops were trialled. The precise details of these protocols are given in the original papers^{18, 46-49}. These included plant sampling protocols to follow the lifecycle of weed plants from the initial seedbank at the start of the year, before crop sowing, to the seedbank after crop harvest. Weed plants were also to be assessed as seedlings at germination, counts during the growing season and biomass protocols just prior to harvest. The amount of seeds set by the standing weeds was assessed between the start of weed flowering and the harvest of the crop. For the invertebrates, Vortis suction sampling and Pitfall trapping were to be done to assess surface active invertebrates and transect walks made to count bees and butterflies. All protocols were conducted within the trial fields (in-field), with some protocols also being done in the surrounding field margins. Weed seedbank and counts protocols were also to be done in follow-up years to assess any long-term effect of GMHT crop management. Crop samples and yield estimates were expressly forbidden from the FSEs by requirement of the UK Government.

The experimental design was the subject of considerable debate. The benefits of a paired-field versus a splitfield design, to contrast the effects of growing a GMHT crop with its conventional crop counterpart, were presented⁵⁰. A split-field design was adopted with the GMHT crop to be grown in one half of the split and a conventional variety of the same crop to be grown in the other. It was also agreed that no attempt was to be made to control the herbicide management of the conventional crop varieties, save for the guidance that the farmer should follow the then current cost-effective weed control. GMHT herbicide management would follow the draft 'label of use' provided by the company commercialising the GMHT crop.

The sampling protocols were to be conducted on up to 12 transects, running from the field margin into the field, in each half of the split field. An initial, pre-trial power analysis was conducted using data gathered from other ecological and agricultural experiments. This examined the statistical power, as the probability of rejecting the null hypothesis when some given alternative hypothesis is true, of different scenarios of split-field numbers for each crop⁵⁰. The analysis suggested that around 60 fields per crop would be sufficient to provide adequate power (80%) for valid statistical inferences of effect on taxa to be made.

Some 66 spring-sown beet, 68 maize, 67 spring oilseed rape and 65 winter-sown oilseed rape fields were studied during the FSE (Supplementary Fig. 6). Each was followed for the one year that the GMHT crop was sown, with approximately 65 fields being studied in each growing season between 2000 and 2003. Field selection criteria included that the field had to be in conventional agriculture, should be of a minimum of 5 Ha (mean = 11 Ha, S.E. = 0.44), assuring the field when split was still of size that was agriculturally relevant, and that the farmer had to have previously grown the conventional crop being considered. The assignment of crops to fields and field halves was random and followed a fully-blind protocol. The farmer also had no role in how the positioning of the split in the field was made.

The sample data were analysed on a taxon by taxon basis using ANOVA⁵⁰. The null hypothesis was tested with a paired randomization test using the treatment effect, d (computed as $d = \log_{10}(GM + 1) - \log_{10}(C + 1)$), for the difference in count for a taxon due to management in the GM and Conventional half-fields. The basic results

for the spring-sown crops were presented in a Special Issue of The Philosophical Transactions of the Royal Society in 2003^{18, 46-48} while the winter-sown oilseed rape results were published in 2005⁴⁹. Headline sample statistics showed that approximately 60,000 field visits were made, sampling some 930,000 plants and 650,000 seeds that were identified to species. Some 2 million invertebrates were sampled, and 24,000 bees and 18,000 butterflies counted on the transect walks. No attempt was made to identify all the invertebrate individuals sampled to species, and the precise taxonomic level and rationale used for each group is presented in the relevant FSE papers. For the Vortis and Pitfall data-sets used in this paper all Carabidae were identified to species. Five taxa of Araneae were identified: the families Linyphiidae and Lycosidae, the genus *Pardosa*, *Erigone* agg. (consisting of *E. atra* and *E. dentipalpis*) and the species *Lepthyphantes tenuis* (*Tenuiphantes tenuis*). All adult Heteroptera were also identified to species. Where possible, all other taxa were identified to family. Notable exceptions were Diptera adults and larvae which are extremely difficult to identify.

The results of the analyses demonstrated that there were significant changes to the amounts of some taxa of weeds, surface dwelling invertebrates and bees and butterflies in the different crops, with some going up and others down in the GMHT. Contemporary and later papers have sought to explain these changes ecologically using species-specific, community and functional approaches^{17,51-53}. Following an independent assessment of the probable risks to biodiversity of adopting GMHT crops, none of the crops were commercialised in the UK.

A retrospective power analysis of the design of the FSEs was conducted to examine whether the trials met their stated power and to identify efficiencies in sampling that might be used in future studies. This showed that "the data collected vindicated the initial statistical power analysis and the planned replication"⁵⁴. *Post hoc* analyses of the split-field design suggests that there is no effect of the dispersal power of a species on the treatment effect observed.

The Vortis and Pitfall sample data

The data used in this paper came from the in-field sampling Vortis and Pitfall sampling protocols^{18,46}.

Plant- and soil-surface active invertebrates were sampled using a Vortis suction sampler. Samples consisted of five 10 second Vortis 'sucks' taken 1 m apart at 2 m and 32 m from the crop edge on three of the twelve transects around each half of the field in June and August, for the spring-sown crops, and September/October and May/June in the winter-sown oilseed rape. Samples were taken when both the soil and the vegetation were dry. Invertebrate samples were stored in a freezer in the laboratory before identification.

Pitfall traps were used to survey populations of soil-surface active invertebrates. The pitfall traps were 6 cm diameter plastic cups sunk into the ground with the top level with the soil surface. Each was two-thirds filled with a 50 : 50 mixture of tap water and ethylene glycol as a sample preservative. Individual traps were positioned at 2, 8 and 32 m from the crop edge along four of the 12 half-field transects. Trapping was done three times on each field: during May, July and August in spring oilseed rape and beet, during late May–early June, July and August in maize and during September/October, April/May and June/July in winter-sown oilseed rape. On each occasion traps were open for two weeks. In the laboratory, the samples were preserved by freezing or in 70% alcohol, before identification under a binocular microscope.

The Vortis and Pitfall data-sets used for the machine learning were year total data, produced by summing the counts from each sample date, for each taxon in each half-field.

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Supplementary Methods 2 | Machine learning ecological networks.

Methods of inferring networks from empirical data include both statistical and logic-based approaches. Attempts have been made to infer ecological networks from time series that record the temporal variation of ecological communities and from contrasted snapshots of the spatial variation in species occurrence or abundance with varying degrees of success⁵⁵⁻⁵⁹. There is much debate about the quality and veracity of the networks learnt using the different statistical methods that are available^{60,61}. To reconstruct the ecological networks analysed here, we explicitly adopted the logic-based machine learning approach, Abductive / Inductive Logic Programming (A/ILP)^{14,36,37}, to reconstruct food-webs directly on the Vortis and Pitfall trap ecological data-sets from the FSE. These logic methods are based on a semantic formalism and differ markedly from statistical approaches⁶². The learning is derived from logic statements^{36,37}, in the form of background knowledge that may prove to circumvent some of the problems associated with the statistical learning that has been done to date⁶².

In our problem, the FSE count data could be represented by variables expressing whether the relative abundance of a taxon in each field is up or down, in the GMHT treatment compared to the conventional. What we wanted to learn was trophic relationships between taxa. We expected that differences in the timing of herbicide management in the Conventional and GMHT field halves would lead to correlated movement or death of invertebrates that are linked trophically. Thus, herbicides applied to one half field would remove weed plant refugia or food resources for an herbivore species, *Y*, which would respond by either moving or dying. A predator of *Y*, species *X*, would then move or die, in turn, due to a similar loss of weed refuge or herbivore food resource, entailing correlated changes in relative abundance as a basic requirement for taxa that are potentially linked via trophic interactions.

To reconstruct an ecological network beyond one of simple correlation, A/ILP uses background knowledge to learn which of these 'correlations' in the data might be trophic as opposed to those that simple arise by chance or due to shared responses to changes in resources, for example. Here, the background knowledge can be looked at as a model for a trophic interaction. Thus, in addition to the basic requirement of correlated changes in relative abundance, our model for a trophic interaction between *X* and *Y* was that: i) both species co-occur within the same samples; ii) species *X* should have a larger body size than *Y* (big things eat small things); and, iii) the predator should also have the appropriate mouthparts for predation. When encoded in the logic programming language Progrol $5.0^{63.64}$, these requirements express the inference that following a management-driven perturbation in the ecosystem, the changed abundance of species *X* and *Y* within any field can be explained by the abductive hypothesis that *X* eats species *Y*.

Progol 5.0 generated a set of abductive hypotheses in the form of eats relations between species separately for the Vortis and Pitfall data-sets. Probability estimates for each of the hypothetical eats relations were computed by direct sampling from the hypothesis space³⁷. These 'eats' trophic links between species could then be presented graphically as weighted ecological networks for each field, for the Vortis and Pitfall protocols. To formally evaluate the predictive power of the hypothetical trophic links, we used a 'leave-one-out' cross-validation test on the observed data for the taxa in the networks. The abundance of each predator at each field site is excluded from a subset of the data, in turn, and we tried to predict whether the abundance of the 'left-out' species went up or down, given the trophic network generated from the remainder of the data. The cross-validation showed that the power of the learning was high^{36,37}.

The veracity of the hypothesized networks was initially examined using a manual literature search, with a specific search for articles noting a realised trophic relationship between species hypothesised to be linked trophically¹⁴. The quality of the information cited varied; in some cases references described direct tests of the hypothesized species interaction using either dissections or molecular tests of gut contents while others related to observations of species with presumed or observed feeding. For the majority of the papers, the evidence for a trophic interaction was anecdotal. We subsequently performed a corroboration of the networks using a specially developed data-mining tool that automatically recovered feeding relationships from web-based reference databases³⁶.

Importantly, the Vortis and Pitfall networks were found to bear all the hallmarks of valid food webs, reflecting the trophic links that appeared in the literature and being appropriate to those expert agro-ecologists questioned.

It was found that links ascribed with high probability by machine learning correlated well with those have multiple references in the literature³⁶.

This did not mean that all the links learnt were expected. Small spiders, such as *Lepthyphantes tenuis* (*Tenuiphantes tenuis*), were found to act as prey in the Vortis and Pitfall networks. Yet the very great majority of spiders, and all those in the two datasets, are obligate predators⁶⁵. The initial concern was that this was a learning artefact of the small size of the spiders, explicitly identifying them via the background knowledge as prey. We directly tested the spider prey trophic links using molecular gut-content analysis methods and it was shown that these apparently illogical, false-positive trophic links were indeed realised with species inferred as predators, such as *Pterostichus melanarius*, preying extensively upon spiders³⁸. This would suggest that the A/ILP machine learning of ecological networks is doing science because: i) the cross-validation power of fit is high; ii) the hypothesised links accord with the literature and agro-ecological expectations; and, iii) A/ILP can hypothesise unknown links that can subsequently be formally tested. Our reconstructed network meets the requirements of ultra-strong learning⁶².

The final step in reconstructing the combined network used for the analysis presented in this paper was to merge the Vortis and Pitfall networks. We hypothesised that the network learnt for a common suite of species should be similar in any valid protocol in which they can be sampled³⁶. Here this meant that for those species that were sampled in both the Vortis and the Pitfall protocols, the links should be similar; the Vortis 'eats' predicates should apply with high predictive power to the Pitfall, and vice versa. We found this to be the case, suggesting that the two protocols contain the same information³⁶; at least as far as shared species. We therefore argued that the sets of relative abundance variables calculated from the Vortis and pitfall sample data could be merged. It should be noted that the food web learnt from merged data is not the same as that constructed by a simple merging of trophic links from the Vortis and the Pitfall networks. The machine learning can infer new trophic links, between taxa present in one data-set as predators of taxa in the other data-set as prey.

The composite ecological network learnt from the merged Vortis and pitfall data-sets, summarised across all fields, contained 72 taxon nodes and 407 trophic edges³⁶. This represents some 25% of the total taxa in the Vortis and pitfall trap data-sets, but accounts for approximately 75% of the abundance of individuals in these protocols.

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Supplementary Figure 1 | **Compositional trophic food webs. a-d**, pairwise conventional and GMHT webs (**a**, beet; **b**, maize; **c**, spring oilseed rape; **d**, winter oilseed rape) with the same species placement between each conventional and GMHT pair. Node size and colour denote the proportion of times a species was found in the given crop variety across all the sites. Nodes bounded by a dark edge are unique to their respective webs.



Supplementary Figure 2 | Correlations in food web size between management. a-d, the size of conventional food webs was plotted against the size of the corresponding GMHT spilt-fields (a, beet (n = 64 fields); b, maize (n = 57); c, spring oilseed rape (n = 65); d, winter oilseed rape (n = 65)). The dashed line denotes the simple linear regression, with the linear regression function and R-square shown. The grey line denotes unity (y = x). **Regression significant at P < 0.001.



Supplementary Figure 3 | Pairwise comparisons on core/periphery substructures in food webs. a-d, one pair of conventional and GMHT webs of a given site (a, beet; b, maize; c, spring oilseed rape; d, winter oilseed rape). Core species in the inner ring are surrounded by periphery species in the outer ring.



Supplementary Figure 4 | Species core presence in food webs. a-d, pairwise conventional and GMHT webs with the same species placement between each conventional and GMHT pair (**a**, beet; **b**, maize; **c**, spring oilseed rape; **d**, winter oilseed rape). Node size denotes the proportion of times a species was found in the given crop variety across all the sites. Colour denotes the gradient of core presence. Species that were always found in the core in both conventional and GMHT are in the inner ring, and similarly, species that were consistently found in the periphery in both conventional and GMHT are in the outer ring. The rest of the species are in the middle ring. Nodes bounded by an edge denote absent species (unfilled) and species that were unique to their respective web (filled).



Supplementary Figure 5 | **Density of links across food webs. a-d**, pairwise comparisons on the rich-club coefficient, ϕ_r , across food webs between conventional (dark thick line) and GMHT (light thin line) are shown for a given site (**a**, beet; **b**, maize; **c**, spring oilseed rape; **d**, winter oilseed rape). Nodes were ordered by their degree which were then normalised by the size of the network to compensate for difference in food web size. Boundaries of the cores are marked by respective vertical lines.



Supplementary Figure 6 | **Map of study fields in the FSEs.** The circles show the locations of the field sites of spring-sown beet, maize and oilseed rape, and winter-sown oilseed rape overlain across Great Britain.









Winter-sown oilseed rape

Spring-sown Beet

Spring-sown Maize

rape

Supplementary Table 1 | **Species and their appearance across sites.** Species are identified by the Biological Records Centre (BRC) code, ranked in a descending order of the total frequency of appearance, and their appearance across sites under each crop variety.

		Beet		Maize		S. oilseed rape		W. oilseed rape		Total
	Total number of sites	64		57		65		65		502
Species	BRC	Conv	GMHT	Conv	GMHT	Conv	GMHT	Conv	GMHT	
Isotomidae	6400 121	64	64	57	57	65	65	65	65	502
Linyphiidae	6708138	64	64	57	57	65	65	65	65	502
Entomobryidae	6400 122	64	64	57	57	64	65	65	65	501
Araneae	6708	62	61	57	57	65	65	65	65	497
Lepthyphantes tenuis	6708 22119	62	60	56	56	64	65	65	65	493
Sminthuridae	6400 22	61	61	57	56	64	64	65	64	492
Pterostichus melanarius	6453 2715	64 50	64	57	56	63	64	61	59	488
Agonum doreglo	6453 2105	59 55	60 59	49	40	53 61	61	62	60 60	450
Carabid larvae	6453 1 8	57	51	46	43	57	58	63	63	443
Aphidoidea	6436	56	51	49	53	61	60	55	55	440
Diptera adults	6447.9	54	49	46	48	57	57	63	63	437
, Notiophilus biguttatus	6453 903	54	51	49	51	51	52	57	56	421
Nebria brevicollis	6453 801	47	43	40	43	55	54	64	63	409
Auchenorhyncha	6434	57	53	44	51	59	48	47	47	406
Loricera pilicornis	6453 1201	41	41	34	43	54	55	61	59	388
Pterostichus niger	6453 2717	51	48	36	36	58	57	42	47	375
Poduridae	6400 111	24	29	39	42	44	51	49	47	325
Curculionidae	6455 94	40	38	13	15	46	52	46	47	297
Bembidion quadrimaculatun	1 6453 2346	37	42	46	47	38	40	15	14	279
Pterosticnus cupreus	6453 2707	31	32	38	34	35	32	38	37	277
Calathus fuscipes	6453 2903	43	45	35	32	31	33	23	24	200
Nebria calina	6453 2000	39 15	12	28	34 25	20	20	22 18	20	203
Rembidion lampros	6453 2326	37	34	20	23	28	23	13	4J 12	194
Agonum muelleri	6453 3513	24	27	20	23	20	24	25	21	186
Demetrias atricapillus	6453 5701	16	15	11	16	22	19	35	38	172
Svnuchus nivalis	6453 3301	31	33	26	20	18	20	7	5	160
Clivina fossor	6453 1402	12	13	15	14	21	22	28	27	152
Bembidion obtusum	6453 2340	24	23	14	14	19	17	19	17	147
Miridae nymphs	6433 84.8	30	22	16	16	22	16	8	10	140
Bembidion guttula	6453 2322	12	13	16	16	15	19	25	23	139
Cimicidae nymphs	6433 82.8	20	15	25	22	22	21	3	0	128
Amara aenea	6453 3701	11	17	11	18	9	10	30	21	127
Bembidion aeneum	6453 2301	11	9	15	12	11	15	25	27	125
Pterostichus strenuus	6453 2720	7	11	10	9	12	13	32	28	122
Stomis pumicatus	6453 2601	19	17	16	15	15	22	7	4	115
Bembidion lunulatum	6453 2330	2	5	16	18	12	15	20	21	109
	6455 66.8	22	25	9	13	14	10	1	5	99
Amara raminans	6453 37 10	4	9	3	2	0	5	32	23	94
Heterontera nymnhs	6433.8	21	9	12	2	9 14	13	6	3	93 85
Nabidae nymphs	6433.81.8	8	5	7	5	20	11	2	0	58
Neuroptera larvae	6439.8	6	8	8	2	10	9	1	2	46
unidentified Coleoptera	6441	16	15	0	0	4	2	0	0	37
Trechus obtusus	6453 2104	9	7	2	2	4	8	3	0	35
Asaphidion stierlini	6453 2204	3	0	1	2	1	1	12	13	33
Onychiuridae	6400 113	1	2	7	9	3	4	1	4	31
Patrobus atrorufus	6453 1702	2	2	0	0	7	7	6	6	30
Metabletus foveatus	6453 6001	6	7	4	6	1	3	0	1	28
Coccinella septempunctata	6455 59604	9	2	3	2	3	3	1	0	23
Amara bifrons	6453 3706	4	3	1	1	4	4	2	1	20
Piesma maculatum	6433 9701	5	5	1	3	1	1	1	1	18
	6453 6002	3	2	3	4	1	1	3	1	18
Anthocoris nemorum	6433 12308	1	0	3	2	4	3	1	1	15
Notionbiluo substriatus	6453 2108	0	2	0	1	3	4	7	4	10
Trechus discus	6453 2101	2	1	3	1	3	3	0	1	14
Dromius linearis	6453 5803	1	1	0	2	1	4	2	3	14
Aaonum obscurum	6453 3515	0	0 0	2	4	3	1	1	1	12
Neuroptera adults	6439.9	3	2	1	3	1	0	1	0	11
Bembidion biguttatum	6453 2307	1	0	1	0	1	0	4	3	10
Propylea quattuordecimpun	ctata 6455 59801	2	1	0	1	3	0	1	0	8
Lygus rugulipennis	6433 20504	1	1	0	1	2	1	0	0	6
Saldula saltatoria	6433 24909	0	0	2	2	1	0	0	0	5
Dyschirius globosus	6453 1304	0	0	1	1	0	0	1	1	4
Leistus rufomarginatus	6453 605	0	1	1	0	0	0	0	1	3
Acupalpus dorsalis	6453 4703	0	0	0	0	0	0	0	2	2
Coccinellidae	6455 66	2	0	0	0	0	0	0	0	2
bradycellus verbasci	6453 4507	U	U	U	U	1	U	U	U	1

Supplementary Table 2 | Analysis of variance on the effects of management and crop type on food web structural properties. Nested ANOVA on the effects of management within each crop type. One-way ANOVA on the effects of crop type among conventional crops. The connectance, relative core size, core link density, ϕ_r , and robustness via random removal and targeted removal are shown. Significant results were further analysed using Fisher's LSD *post hoc* tests.

	Crop type				Management					
	df	SS	MS	F _{3, 247}	Р	df	SS	MS	F _{4, 247}	Р
Connectance	3	0.004	0.001	2.38	0.070	4	0.006	0.001	2.79	0.023*
Relative core size	3	0.143	0.048	4.87	0.002 †	4	0.032	0.008	0.98	0.416
Core link density ϕ_r	3	0.064	0.021	6.80	<0.001‡	4	0.009	0.002	1.04	0.386
Robustness via random removal	3	0.002	0.001	2.54	0.057	4	0.005	<0.001	0.72	0.575
Robustness via targeted removal	3	0.024	0.008	2.93	0.034§	4	<0.001	0.001	0.61	0.654

Significant results highlighted in bold

* GMHT beet > conventional beet

† Maize > beet; maize > winter oilseed rape

 \ddagger Winter oilseed rape > maize; winter oilseed rape > spring oilseed rape

§ Winter oilseed rape > beet.

Supplementary Table 3 | Comparisons of the taxonomic composition in the core and periphery.

	Be	eet	Ма	ize	Spring oi	seed rape	Winter oilseed rape		
Common core species	13.81 ± 2.86		14.46 ± 3.81		14.55	± 3.16	14.48 ± 2.95		
Common periphery species	5.41 ± 2.51		4.12 ± 2.18		4.92 ± 2.02		5.54 ± 1.99		
Conv core and GMHT periphery	0.86 ± 1.17		1.23 ± 1.64		1.29 ± 1.78		0.85 ± 1.20		
Conv periphery and GMHT core	0.95	± 1.37	0.88	± 1.23	0.98	± 1.17	1.29 ± 1.73		
	Conv	GMHT	Conv	GMHT	Conv	GMHT	Conv	GMHT	
Core species in respective web only	1.80 ± 1.51	1.69 ± 1.25	1.95 ± 1.51	2.00 ± 1.27	1.69 ± 1.41	2.05 ± 1.45	1.57 ± 1.37	1.42 ± 1.17	
Periphery species in respective web only	2.69 ± 1.77	2.14 ± 1.68	2.19 ± 1.61	2.47 ± 1.90	2.38 ± 1.81	2.06 ± 1.50	2.25 ± 1.50	1.77 ± 1.30	

For a given crop, the percentage of common core and periphery species were compared. A small proportion of species were found in the core in the conventional webs but in the periphery in the GMHT counterparts. Also, a small proportion of core and periphery species were only found in their respective web, i.e. species that only in a given variety of a given crop and not in their counterpart.