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ABSTRACT

Sustainable management of ecosystems and growth in agricultural productivity is at the heart of the United Nations' Millennium Development Goals for 2030. New management regimes could revolutionise agricultural production, but require a full evaluation of potential risks and opportunities. Replacing existing conventional weed management with genetically modified, herbicide-tolerant crops (GMHT), for example, might reduce herbicide applications and increase crop yields, but remains controversial owing to concerns about potential impacts on biodiversity. To date, such new regimes have been assessed at the species or assemblage level, whereas higher-level ecological network effects remain largely unconsidered. Here, we conduct a large-scale network analysis of invertebrate communities across 502 UK farm sites to GMHT management in different crop types. We find that network-level properties were overwhelmingly shaped by crop type, whereas network structure and robustness were apparently unaltered by GMHT management. This suggests that taxon-specific effects reported previously did not escalate into higher-level systemic structural change in the wider agricultural ecosystem. Our study highlights current limitations of autecological assessments of effect in agriculture in which species interactions and potential compensatory effects are overlooked. We advocate adopting the more holistic system-level evaluations we pioneer here, which complement existing assessments for meeting our future agricultural needs.

INTRODUCTION

Developing management that conserves biodiversity whilst delivering the services we need from ecosystems without introducing further harm is a pressing issue for the future of human societies[1,2,3]. The demand for sustainable food security and ecosystem services[4] in the face of global change and biodiversity loss due to current farming regimes, means new agricultural management practices[1] will be needed, based on sound ecological understanding[5]. In agro-ecosystems, assessment of new practices concentrates primarily on risks to biodiversity, and therefore aims to evaluate whether a novel management has an adverse effect on the abundance and diversity[6] of individual species or taxa against the noisy backdrop of natural variation. However, if our aim is to manage agro-ecosystems for optimum delivery of ecosystem services, such a focus may be too narrow[7]. Not only does this approach tend to disregard benefits of the new management to crop yield and quality, but also, and more importantly for our purposes here, it may consider any change in

biodiversity as posing unacceptable risk[8]. Such conservatism in risk assessment stems in large part from a lack of universal methods to evaluate the importance of structural and functional effects that changes in biodiversity can be triggered via indirect effects that ripple through networks of interacting species. Moreover, many studies suffer from a lack of replication[9], leading to incomplete or inaccurate estimations of potential ecological risks[5].

Ecological network approaches have been advocated as part of the next generation of biomonitoring tools[10,11] because they can capture the underlying functioning and dynamics emerging from complex species interactions[12], whereas the traditional evaluation methods that focus on a few taxa can mask these higher-level and often indirect synergistic or compensatory effects[13]. By elucidating the wider system, network approaches could open the way to improving productivity while safeguarding biodiversity and ecosystem services in agriculture via better decision-making based on more holistic, structural assessments. To date the low number of highly resolved ecological networks has impeded their application in real-world agro-ecosystems. The recent emergence of machine learning and molecular biological techniques provides new methodologies for constructing large-scale replicated networks[11,14], although system-level responses to change remain mostly unexplored.

Here we perform a large-scale assessment on agro-ecosystem responses by analysing a case study of 502 replicated food webs, from fields of the Farm Scale Evaluations (FSE) of genetically modified, herbicide-tolerant (GMHT) crops[15] (Methods and Supplementary Methods 1). The case study data-set is of in-field Vortis suction and Pitfall sampled invertebrates from 251 fields of four widely grown crops, in a spilt-field design in which conventional and GMHT varieties were grown alongside one another. From each half of the split-field, we constructed a food web of species trophic relationships (Methods and Supplementary Methods 2). Switching crops commonly causes biodiversity change in farmland[16] but it is widely accepted as part of traditional crop rotations, whereas the adoption of GMHT represents an alternative form of (future) management. Previous FSE analyses have assessed farming biodiversity by focusing on species-specific measures[15,17], such as changes in invertebrate populations indirectly driven by herbicide management of weed plants, which can be sensitive to the inherent noise or the contingency of responses[13,18] and functional traits[19].

We quantified the overall effects of crop types and GMHT management on the agro-community via a network-based approach to gauge potential changes in food web structure and robustness (Methods).

RESULTS & DISCUSSION

The dominant first-order effect was crop type (Fig. 1a, b, Supplementary Fig. 1 and Supplementary Table 1), with a common suite of interconnected species evident in most field-sites, including typical farmland taxa such as the carabids, *Pterostichus melanarius*, the detritivore collembolans of the Entomobryidae and Isotomidae, and the linyphiid spider, *Lepthyphantes tenuis* (*Tenuiphantes tenuis*). Species dissimilarity (diversity) was high among crop types, but noticeably lower when conventional crops were compared with their GMHT counterparts (Fig. 1c) reflecting the greater differences of environmental conditions provided to invertebrate species in the different crops[8]. The food webs of a given crop variety (e.g. conventional beet or GMHT maize) varied greatly in size among sites; however, the conventional and GMHT webs always remained highly correlated within sites (Supplementary Fig. 2).

Species turnover can significantly alter food web structure and dynamics, particularly where incoming and outgoing nodes have markedly different links due to variation in their diet or consumers[20]. A commonly used structural metric of web complexity, connectance, was unchanged by crop type, but was significantly greater under GMHT (Nested ANOVA $F_{4,247} = 2.79$, $P = 0.023$; Supplementary Table 2), which appears to be due to an increase in links in the GMHT to the Collembola. Network theory suggests that higher levels of structural complexity can confer food web stability, if most interactions are relatively weak[21], and there is growing evidence to support this in ecological networks[22]. However, such crude whole-network metrics can be relatively insensitive to important but more subtle changes that may arise within the web, and newer substructural measures can provide deeper insights here[20]. For instance, cores are a cohesive substructure of highly connected nodes that are said to govern the dynamics and functioning of complex systems, and their densely intertwined pathways can provide redundancy to buffer external perturbations and maintain food web robustness[20,23]. We extracted the core properties[20] of the webs to evaluate whether network substructures responded to farming regime. All the 502 food webs possessed cores surrounded by loosely connected peripheral species (Supplementary Fig. 3), revealing a previously unknown but recurrent core-motif

(community) of species in agro-ecosystems that could be key for driving ecosystem properties[24]. Crop type resulted in significant variation in species composition in the substructures, and especially for peripheral species (Fig. 2a, b). Substructuring, both in terms of organisation and composition, appeared to be largely unaffected by GMHT management (Fig. 2c, d), again suggesting negligible impacts at these higher organisational levels. In particular, the conventional and their GMHT counterpart webs shared significant numbers of core and periphery species, with the species in the cores tending to be those that were common across sites (Fig. 2c, d, Supplementary Fig. 4), such as the *Isotomidae* collembola.

Relatively large cores were observed across all the food webs, accounting for 65-71% of total species richness on average (Supplementary Table 3), and these findings are similar to that observed in aquatic ecosystems when comparing natural networks with others[20]. The core size was strongly affected by crop type (Nested ANOVA $F_{3,247} = 4.87$, $P = 0.002$; Supplementary Table 2), but was unchanged by GMHT management (Nested ANOVA $F_{4,247} = 0.98$, $P = 0.416$; Supplementary Table 2). The link density within the core, gauged by the rich-club coefficient[20], varied significantly among crop types (Nested ANOVA $F_{3,247} = 6.80$, $P < 0.001$; Supplementary Table 2), but was again unaltered by GMHT management (Supplementary Fig. 5; Nested ANOVA $F_{4,247} = 1.04$, $P = 0.386$; Supplementary Table 2). Changes in core size and core link density, here induced by the crop type, are common network responses to external disturbance[25] (e.g. a stressor can reduce core size which in turn results in lesser number of alternative paths within a food web for exchanges of energy fluxes) which can potentially impact network redundancy[26] and robustness.

Altering agricultural practice could reshape the taxonomic and network properties of ecosystems and their response to further external disturbance, such as biodiversity loss caused by current intensive agricultural management[5]. To assess food web robustness, we applied two simple but common simulated scenarios of species loss: random versus a risk scenario of targeted high-degree node removal, with the former representing a "null model" and the latter mimicking the supposed 'worst-case' loss of highly connected keystone species[27] (Methods). The major differences were once again manifested between crop types, especially under targeted removal (Nested ANOVA $F_{3,247} = 2.93$, $P = 0.034$, Supplementary Table 2). These findings illustrate how crop type determines network properties that can potentially compromise the overall structural integrity and the

ecosystem's ability to buffer the effect of taxonomic loss or turnover. In both scenarios, conventional and GMHT crops responded in the same way (Supplementary Table 2), reflecting their homologous network structures.

Our large-scale evaluation revealed network-level responses of GMHT crops are remarkably similar in their composition, structure and responses to simulated trajectories of species removals, to their conventional counterparts (Fig. 3). This suggests that previously recorded changes in taxa traits[8] may be compensated for at these higher organisational levels, due to prevalent trophic redundancy. Cultivating crops in rotational sequences is integral to farming and we found that crop type was by far the dominant driver of differences in web structure and robustness, across several organisational levels, ranging from substructural to whole-network attributes; inter-annual variation is likely greater than differences between conventional and GMHT. This demonstrates how traditional autecological analysis, which treats species as fixed taxonomic identities with defined traits provides only a partial view of the potential ecological consequences of a change in management. Despite the realised economical and environmental benefits of transgenic crops[28], their planting continues to raise controversy in terms of perceived ecological and environmental risk, and this has restricted their adoption in some parts of the world[29]. Our case study demonstrates that the changes in pitfall and Vortis sampled species abundance recorded in GMHT crops previously[8] would have been less likely to be interpreted as a systemic and potentially critical risk to the agricultural ecosystem if network-based approaches had been included from the outset. The food web variation due to the GMHT could also have been set within the natural variation of the conventional crops currently accepted in UK farmland. This case study does not, however, examine all the taxa that exist in the FSE data (Supplementary Methods 1), notably not evaluating the effects of GM herbicide management on networks of pollinators, which are of considerable interest worldwide. Reconstructing networks for these other taxa from the FSE would test whether observed changes in species-specific abundances[8] translate to changes in network structure and ecosystem change and might modify the conclusions of this case study.

Previous studies on agro-ecosystems have focused on far smaller experimental designs with limited replication, restricted spatial scale and a focus on the lower organisational levels when assessing how agricultural practices

affect biodiversity and ecological risks. Here we show explicitly that network-based approaches can reveal synecological attributes that are central to understanding the multispecies responses of an ecosystem and its potential robustness. With the global drive to conserve ecosystems and their services, including attaining long-term food security[6,30] by adopting more sustainable management approaches, advances in management need to be coupled with comprehensive change detection and evaluation methodologies and criteria and baselines for ecosystem risk assessment. Our case study shows how replication-explicit, network-based tools could aid future evaluations of ecosystem change that are better able to capture the underlying biocomplexity of nature. In principle, biomonitoring and risk management decisions based upon networks ought to be more robust than those based alone on statistically significant effects on individual taxa, some of which may arise spuriously with multiple comparisons.

The practicalities of using network analysis in decision-making about agricultural practices need careful consideration. Using current methods, a programme the size of the FSE would be impractical for decision-making about the use of individual products, such as a new GM crop variety or a new pesticide formulation. While the collection and analysis of data will likely become easier, for example through the use of eDNA[11], the size and duration of the experiments may prove too much for pre-market product regulation. We envisage three scenarios where network analysis may be valuable. First, FSE-like experiments could be useful in decision-making over the introduction of a new management technique or class of products that will be used extensively; the adoption of winter-sown cereals and GMHT crops are examples of such widespread changes. Second, network analysis could be used as a risk management tool after the introduction of a new management regime; for example, the regime could be introduced on a limited area and network analysis used to assess whether its ecological effects are acceptable; in effect, limited commercial use of a method would act like an FSE. Finally, network analysis could be used to check the cumulative effects of products under current regulations and used to test whether risk-assessment of species effects predict the resilience of ecosystem-service delivery by agro-ecosystems. These analyses could contribute to debates about the roles of species diversity[31], higher order interactions[32] and landscape[33] on agro-ecosystem functioning when viewed through the lens of ecological networks[34]. Results of such analyses could help to improve the design of "low-tier" laboratory studies and build

an ecologically-based assessment framework that would better predict ecosystem effects from changes in the life-history parameters of single species.

METHODS

Farm Scale Evaluations (FSE). The FSE[15] was a three-year study involving the analysis of the effects of GMHT crops to the farmland biodiversity across the UK, and the details of farmland selection and crop field design are described more fully elsewhere[35]. To summarise, a split-field design was used in 64 beet (B), 57 maize (M), 65 spring-sown oilseed rape (SR) and 65 winter-sown oilseed rape (WR) sites (Supplementary Methods 1). Each crop field was split approximately in half and a conventional and GMHT variety of one of the crops assigned randomly to each half[15,35]. Species were sampled using Vortis suction and pitfall sampling, and taxa identity and abundance information were recorded within the field across all the sites.

Food web construction. FSE field sample data on taxa and the background information on species traits (e.g. body size and feeding type) were used to generate hypotheses in the form of trophic relationships between species (i.e. food-webs) using a logic-based machine learning approach called Abductive / Inductive Logic Programming (A/ILP) implemented in the Progol 5.0 language (Supplementary Methods 2)[14,36,37]. The method aims to attain the best explanation of the data based on the generated hypotheses and produces the most plausible predation relationships that can exist among all the species recorded in FSE Vortis and pitfall trap datasets. These predation links have been validated in empirical studies and the predictive accuracy of the method was found to be significantly higher than other non-probabilistic techniques[14,36–38]. Based on the sampled taxonomic information of each half of the spilt-field in FSE, we constructed replicated food-webs using inferred trophic links generated by the A/ILP machine learning, and obtained a total of 502 food webs.

Impacts of agricultural practice on food web size. We evaluated the differences in the taxonomic composition among crop types and management varieties by referring to their aggregated compositional webs, which takes both the species and their frequency of appearance across all spilt fields into account. A total of eight aggregated webs were obtained, e.g. conventional beet or GMHT maize, etc. We then applied the Bray-Curtis index[39], b, to quantify the compositional similarity between two aggregated webs with reference to the

total counts of each species obtained from these webs; with $b = 0$ as the most similar and $b = 1$ as the most dissimilar. To examine the correlations in web size between conventional webs and their GMHT counterparts, individual food webs from each half of the spilt-fields were used and linear regression was applied.

Impacts of agricultural practice on food web structure. We measured directed connectance of individual food webs from each half of the spilt-fields, L/S^2, where L is the number of links and S is the number of species, which is a common measure of food web complexity, reflecting its robustness in response to external disturbance[27]. We applied complex network analysis to characterise the substructural properties of all the individual food webs. A network core refers to a cohesive substructure[20,40] that consists of high degree (highly connected) species which are well interconnected with each other. We hypothesized that food webs in this study also exhibit this substructural property and applied a profiling technique[23] to define the cores in individual food webs. Nodes were ordered in descending order of their degree. A node with a rank r has degree k_r, and the number of links that this node shares with nodes of a higher rank is k_r^+. We examined k_r^+ as a function of r and the core is defined by the node with rank r^* where k_r^+ reaches its maximum (i.e. $k_{r*}^+ > k_r^+$ for $r > r^*$), indicating a change in the interconnectedness among high degree nodes. To compare the species composition in the web cores between crop types and management, here again, we aggregated all the core species and their frequency found in the cores across all spilt-fields and quantified the overall similarity using the Bray-Curtis index. We repeated this analysis for the peripheral species composition.

Core size of a network is defined as S_C/S, where S_C is the number of species in the core and S is the total number of species. This core property indicates a system's state: a large core is associated with a greater level of redundancy within a system, which can mitigate the effect of external disturbance. On the other hand, stress in a system is often manifested as a core of reduced size[25,41,42]. We measured the density of links within the core by calculating the rich-club coefficient[43], ϕ_r, which is given by:

$$\phi_r = \frac{2}{r(r-1)} \sum_{i=1}^{r} k_i^+ = \frac{2E_r}{r(r-1)}$$

where E_r is the number of links shared by the highest ranked r nodes and $r \cdot (r - 1) / 2$ is the maximum number of possible links among these nodes. The connectivity of a core is given by ϕ_{r*} whereby a fully connected core has a value of $\phi_{r*} = 1$ and a fully disconnected core gives $\phi_{r*} = 0$.

Impacts of agricultural practice on food web robustness. The architecture of food webs governs their robustness and underpins their response to external disturbance[44]. We studied the potential effect of compositional, structural and substructural changes on network robustness using two simple but common species removal scenarios, with no network link rewiring and evaluated the rate at which the network collapsed[27]. Firstly, species were removed at random at each simulation step, and the total species extinction is the sum of primary loss and secondary loss as a result of species isolation from resource. We measured the robustness for each web by recording the proportion of primary species loss resulting in a total extinction (primary and secondary) of 50% of the species[27,45]. For each food web, we ran the random removal simulation for 100 times and results were averaged (within a standard deviation $\sigma = 0.076$). Secondly, species were removed sequentially in descending order of degree to simulate the worst-case of loss of the most connected taxa. When a node was removed from a food web, the degrees among the rest of the nodes were also altered, and therefore, we re-calculated the degree order after each node removal. Again, we measured robustness as the amount of primary taxa loss in order to generate a total of 50% species extinction.

Statistical analysis. To test the effects of management practices associated with each crop variety (conventional or GMHT) we used a Type I ANOVA with crop variety nested within crop type. To account for pseudo-replication, an error structure with each spilt-field nested within each site was used. To test the effects of management practices associated with each crop type, we used a Type II one-way ANOVA on conventionally managed food webs only. We applied both models to food web properties (connectance), substructural network properties (core size and core link density), and food web robustness (both random and targeted species removal). Significant results were followed by Fisher's LSD *post hoc* test to identify the contributing factors.

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Figure 1 | Variations in taxonomic composition. Compositional trophic food webs of maize (shown as a representative example of the four crop types). **a**, conventional; **b**, GMHT variety. The same species placement is used in both cases. 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 (i.e. were only found in either conventional or GMHT spilt-fields). **c**, Comparisons of species dissimilarity between crop types and management using the Bray-Curtis dissimilarity index. Colour denotes the degree of dissimilarity with $b = 0$ as the most similar and $b = 1$ as the most dissimilar.
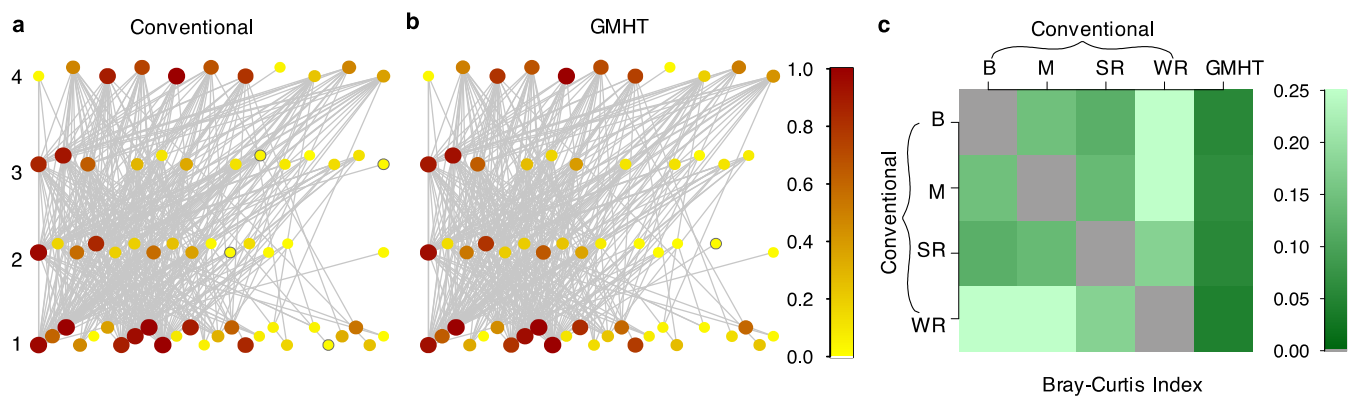
Figure 2 | Core/periphery substructures in food webs. Comparisons of species composition between crop types and GMHT management using the Bray-Curtis dissimilarity index. **a**, Core species; **b**, Peripheral species. **c - d,** Pairwise compositional webs of maize (**c**, conventional; **d**, GMHT). The same species placement is used in both cases. 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. Nodes that were found in both the core and the periphery are in the middle ring. Nodes bounded by an edge denote absent species (unfilled) and species that were unique to their respective web (filled).
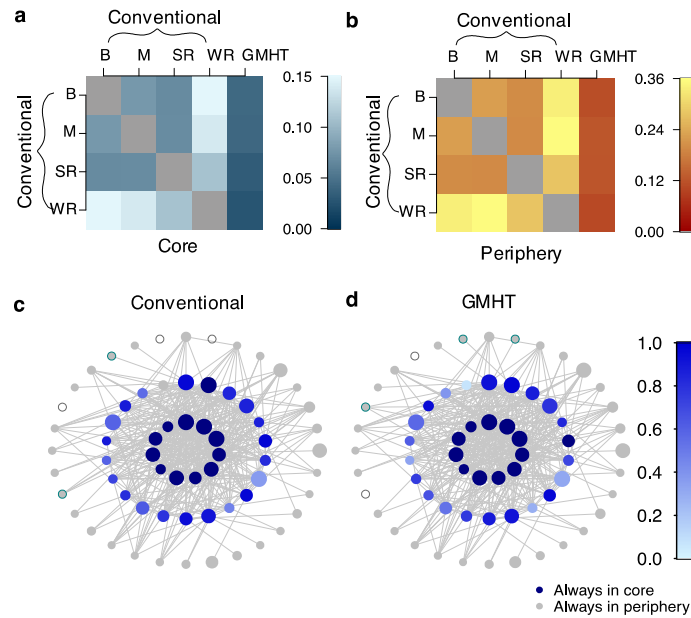
Figure 3 | Food web properties varied significantly between crop types. a – h, pairwise comparisons between management varieties (**a,b**, beet; **c,d** maize; **e,f**, spring oilseed rape; **g,h**, winter oilseed rape). *C*, connectance; ϕ, core link density; core size; R_R, robustness via random removal and R_T, robustness via targeted removal of highest degree nodes are shown (Methods). Each metric is averaged across all webs of a given variety and normalised by its overall range. The effects of crop type can be visualised by comparing results from conventional crops horizontally.
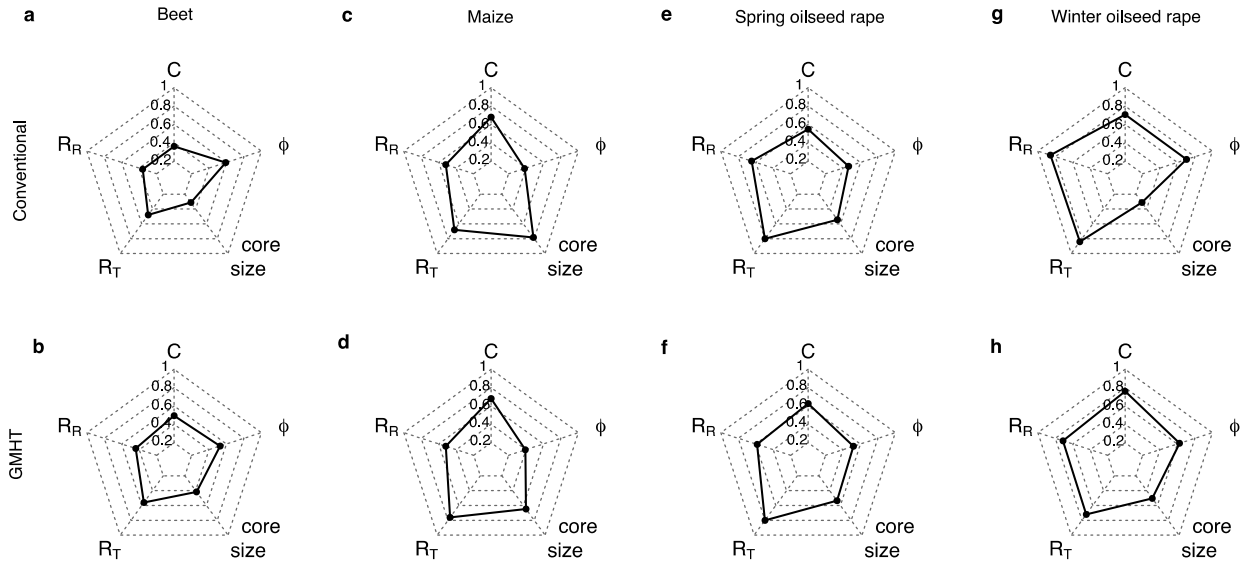
Extended Data Figure 1 | Compositional trophic food webs. a-d, pairwise conventional and GMHT webs (**a**, beet; **b**, maize; **c**, spring oilseed rape; **d**, winter oilseed rape) with the same species placement between each conventional and GMHT pair. Node size and colour denote the proportion of 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.
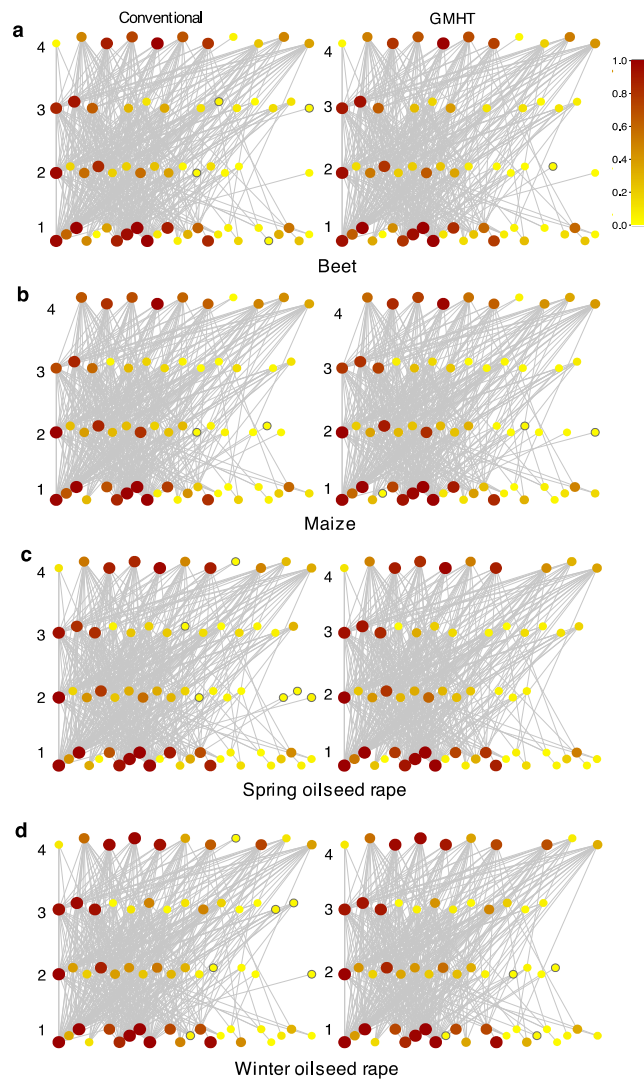
Extended Data Figure 2 | Correlations in food web size between management. a-d, the size of conventional food webs was plotted against the size of the corresponding GMHT spilt-fields (**a**, beet; **b**, maize; **c**, spring oilseed rape; **d**, winter oilseed rape). The dashed line denotes the linear regression, with the linear regression function and R-square shown. The grey line denotes unity (y = x). ***Regression significant at $P < 0.001$.
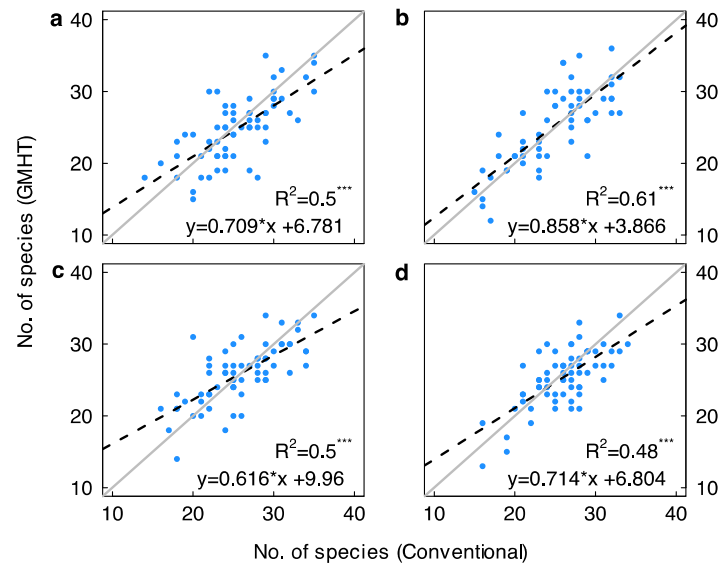
Extended Data Figure 3 | Pairwise comparisons on core/periphery substructures in food webs. a-d, one pair of conventional and GMHT webs of a given site (**a**, beet; **b**, maize; **c**, spring oilseed rape; **d**, winter oilseed rape). Core species in the inner ring are surrounded by periphery species in the outer ring.
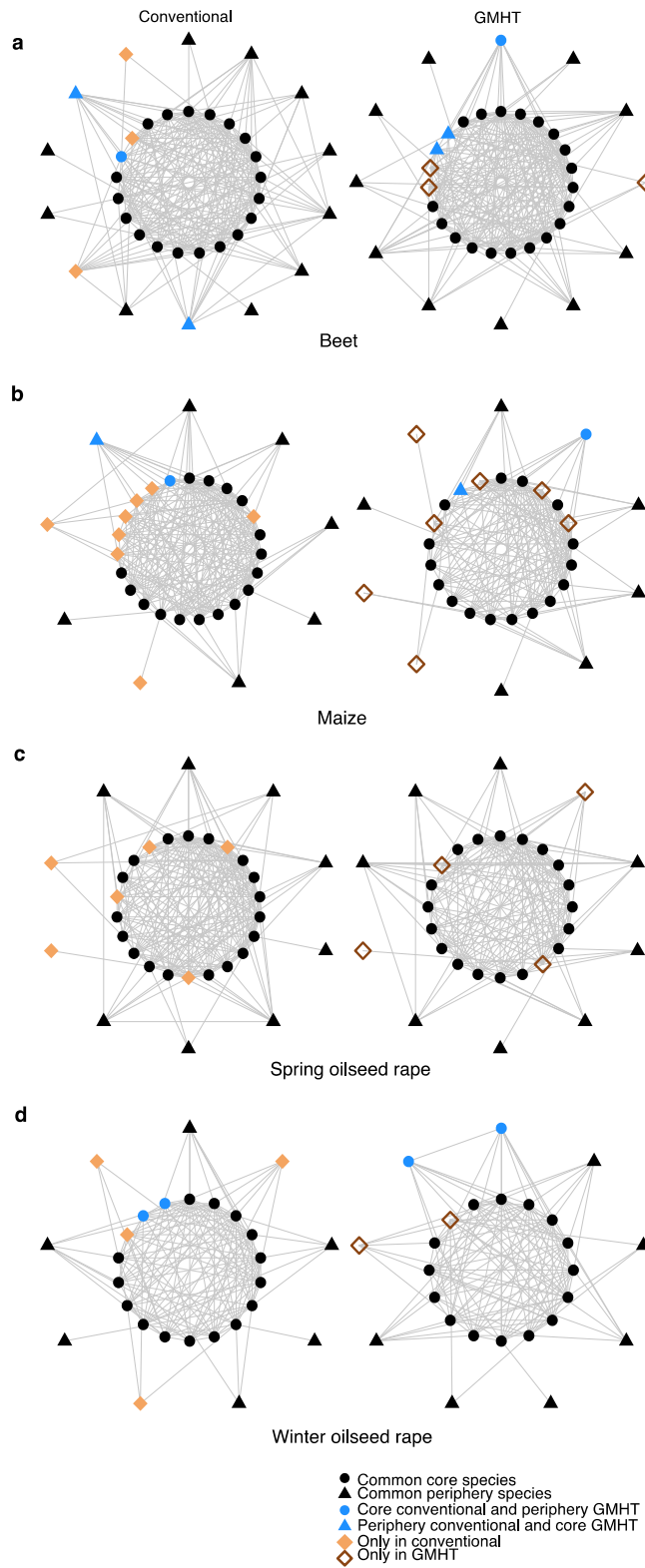
Extended Data Figure 4 | Species core presence in food webs. a-d, pairwise conventional and GMHT webs with the same species placement between each conventional and GMHT pair (**a**, beet; **b**, maize; **c**, spring oilseed rape; **d**, winter oilseed rape). Node size denotes the proportion of times 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).
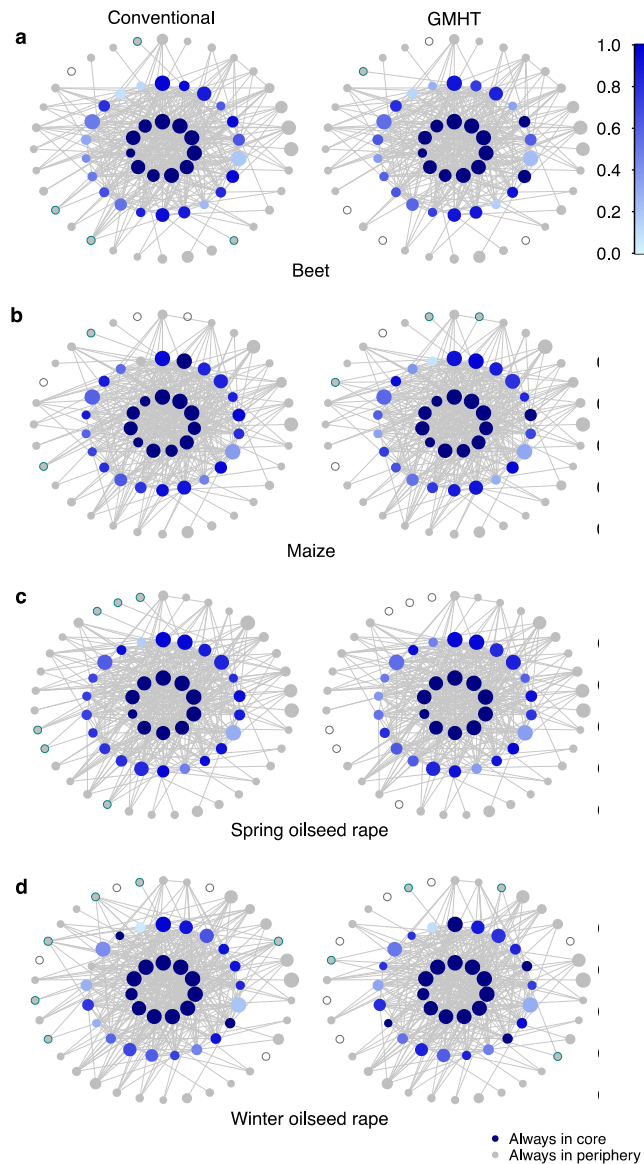
Extended Data Figure 5 | Density of links across food webs. a-d, pairwise comparisons on the rich-club coefficient, ϕ_r, across food webs between conventional (dark thick line) and GMHT (light thin line) are shown for a given site (**a**, beet; **b**, maize; **c**, spring oilseed rape; **d**, winter 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.
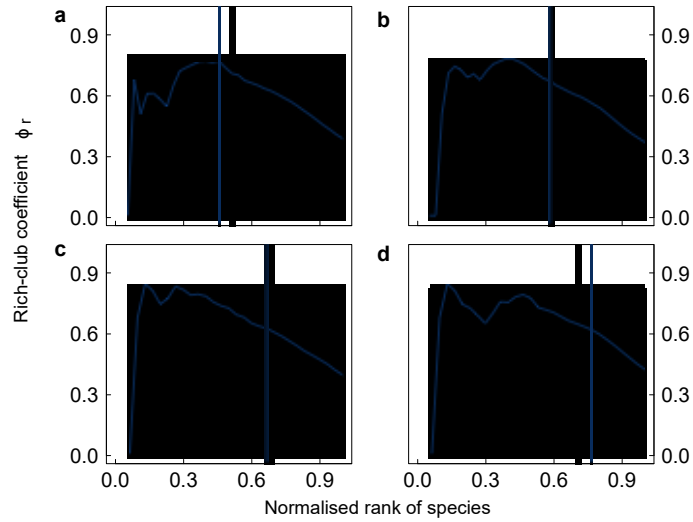
Extended Data Table 1 | Species and their appearance across sites. Species are identified by the Biological Records Centre (BRC) code, ranked in a descending order of the total frequency of appearance, and their appearance across sites under each crop variety.

		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	64	57	56	63	64	61	59	488
Trechus quadristriatus	6453 2105	59	60	49	46	53	60	63	60	450
Agonum dorsale	6453 3503	55	58	41	45	61	61	62	60	443
Carabid larvae	6453 1.8	57	51	46	48	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 quadrimaculatum	6453 2346	37	42	46	47	38	40	15	14	279
Pterostichus cupreus	6453 2707	31	32	38	34	35	32	38	37	277
Calathus fuscipes	6453 2903	43	45	35	32	31	33	23	24	266
Bembidion tetracolum	6453 2355	39	41	38	34	28	35	22	26	263
Other Coleoptera	6441.9	35	38	34	28	30	33	20	22	240
Nebria salina	6453 806	15	12	28	25	32	29	48	45	234
Bembidion lampros	6453 2326	37	34	22	21	28	27	13	12	194
Agonum muelleri	6453 3513	24	27	20	23	22	24	25	21	186
Demetrias atricapillus	6453 5701	16	15	11	16	22	19	35	38	172
Synuchus 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
Coccinelid larvae	6455 66.8	22	25	9	13	14	10	1	5	99
Amara familiaris	6453 3716	4	9	3	7	11	5	32	23	94
Leistus spinibarbis	6453 606	8	7	1	2	9	3	32	31	93
Heteroptera nymphs	6433.8	21	9	12	7	14	13	6	3	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
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
Metabletus obscuroguttatus	6453 6002	3	2	3	4	1	1	3	1	18
Anthocoris nemorum	6433 12308	1	0	3	2	4	3	1	1	15
Trechus secalis	6453 2108	1	2	0	0	3	4	1	4	15
Notiophilus substriatus	6453 908	0	0	3	1	1	0	7	2	14
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
Agonum obscurum	6453 3515	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 quattuordecimpunctata	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	0	0	0	0	1	0	0	0	1

Extended Data 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*	$F_{3,\,247}$	*P*	*df*	*SS*	*MS*	$F_{4,\,247}$	*P*
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

‡ Winter oilseed rape > maize; winter oilseed rape > spring oilseed rape

§ Winter oilseed rape > beet.

Extended Data Table 3 | Comparisons on the taxonomic composition in the core and periphery.

	Beet		Maize		Spring oilseed 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.