

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

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Sustainable management of ecosystems and growth in agricultural productivity is at the heart of the United Nations' Sustainable Development Goals for 2030. New management regimes could revolutionize agricultural production, but require an evaluation of the risks and opportunities. Replacing existing conventional weed management with genetically modified, herbicide-tolerant (GMHT) crops, for example, might reduce herbicide applications and increase crop yields, but remains controversial owing to concerns about potential impacts on biodiversity. Until now, 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 that we explore here, which complement existing assessments for meeting our future agricultural needs.

Developing management that conserves biodiversity while delivering the services we need from ecosystems without introducing further harm is a pressing issue for the future of human societies^{1–3}. The demand for sustainable food security and ecosystem services⁴ in the face of global change and biodiversity loss due to current farming regimes means new agricultural management practices¹ will be needed, on the basis of sound ecological understanding⁵. 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 diversity⁶ 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 narrow⁷. 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 risk⁸. Such conservatism in risk assessment stems in large part from a lack of universal methods to evaluate the importance of structural and functional effects and a lack of understanding 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 replication⁹, leading to incomplete or inaccurate estimations of potential ecological risks⁵.

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 interactions¹², whereas the traditional evaluation methods that focus on a few taxa can mask these higher-level and often indirect synergistic or compensatory effects¹³. 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 on the basis of more holistic, structural assessments. So far, 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 GMHT crops¹⁵ (Methods and Supplementary Methods 1). The case study dataset is of in-field Vortis suction and Pitfall sampled invertebrates from 251 fields of four widely grown crops, in a split-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 farmland¹⁶ 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 traits¹⁹. 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).

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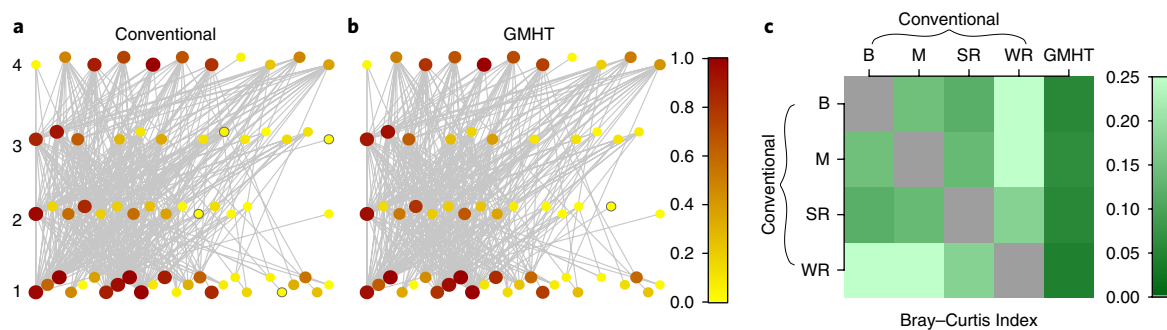


Fig. 1 | Variations in taxonomic composition. **a,b**, Compositional trophic food webs of maize (shown as a representative example of the four crop types). **a,b**, Conventional maize (**a**) and GMHT variety (**b**). The same species placement is used in both cases. Node size and colour denote the proportion 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 (that is, they 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. B, beet; M, maize; SR, spring-sown oilseed rape; WR, winter-sown oilseed rape.

Results and 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 carabid, *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 crops⁸. The food webs of a given crop variety (for example, 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 greatly alter food web structure and dynamics, particularly where incoming and outgoing nodes have markedly different links due to variation in their diet or consumers²⁰. A commonly used structural metric of web complexity, connectance, was unchanged by crop type, but was significantly greater under GMHT (nested analysis of variance (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 weak²¹, and there is growing evidence to support this in ecological networks²². 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 here²⁰. 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 properties²⁰ 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 properties²⁴. 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 organization and composition, appeared to be largely unaffected by GMHT management (Fig. 2c,d), again suggesting negligible impacts at these higher organizational levels. In particular, the conventional and their

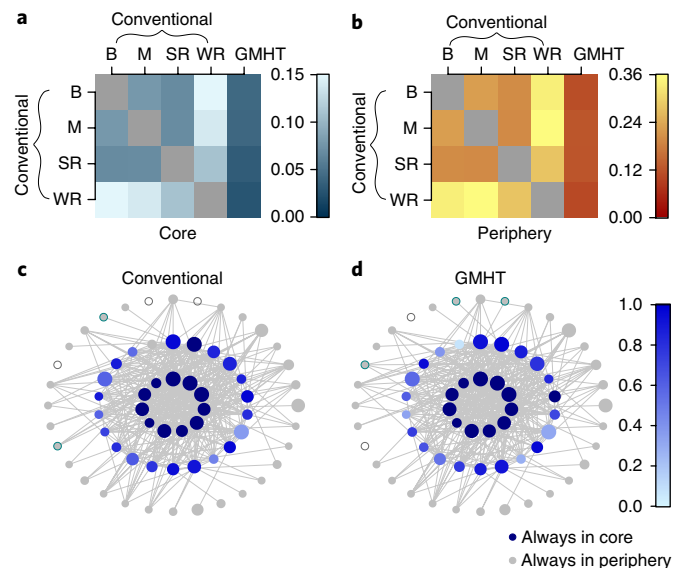


Fig. 2 | Core/periphery substructures in food webs. Comparisons of species composition between crop types and GMHT management using the Bray-Curtis dissimilarity index. **a**, Core species. **b**, Peripheral species. **c,d**, Pairwise compositional webs of maize (**c**, conventional; **d**, GMHT). The 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).

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 and 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

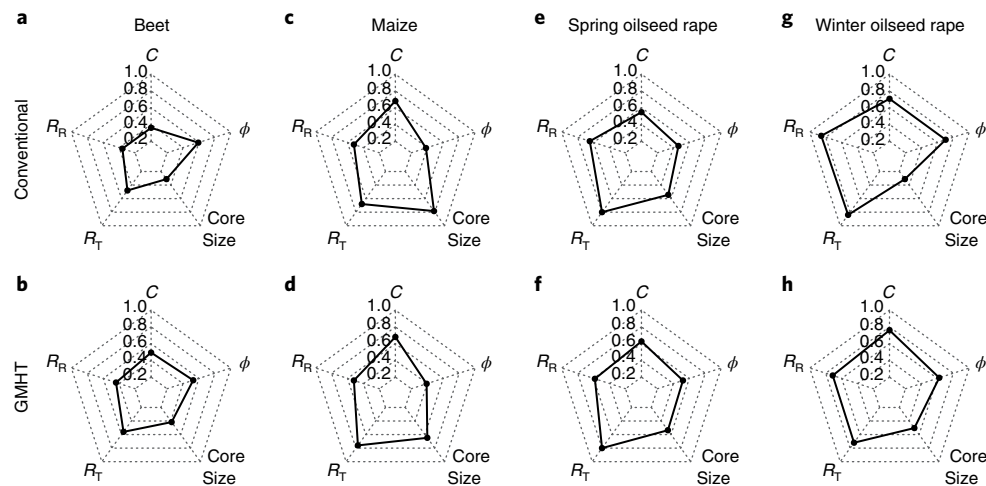


Fig. 3 | Food web properties varied significantly between crop types. **a–h**, Pairwise comparisons between management varieties (**a,b**, beet; **c,d**, maize; **e,f**, spring oilseed rape; **g,h**, winter oilseed rape). *C*, connectance; ϕ , core link density; core size; R_R , robustness via random removal and R_T , robustness via targeted removal of highest degree nodes are shown (see Methods). Each metric is averaged across all webs of a given variety and normalized by its overall range. The effects of crop type can be visualized by comparing results from conventional crops horizontally.

with others²⁰. The core size was strongly affected by crop type (nested ANOVA $F_{3,247} = 4.87$, $P = 0.002$ and Supplementary Table 2), but was unchanged by GMHT management (nested ANOVA $F_{4,247} = 0.98$, $P = 0.416$ and Supplementary Table 2). The link density within the core, gauged by the rich-club coefficient²⁰, varied significantly among crop types (nested ANOVA $F_{3,247} = 6.80$, $P < 0.001$ and Supplementary Table 2), but was again unaltered by GMHT management (Supplementary Fig. 5, nested ANOVA $F_{4,247} = 1.04$, $P = 0.386$ and Supplementary Table 2). Changes in core size and core link density, here induced by the crop type, are common network responses to external disturbance²⁵ (for example, 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) that can potentially impact network redundancy²⁶ 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 management⁶. 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 species²⁷ (Methods). The major differences were once again manifested between crop types, especially under targeted removal (nested ANOVA $F_{3,247} = 2.93$, $P = 0.034$ and 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 traits⁸ may be compensated for at these higher organizational 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 organizational levels, ranging from substructural to whole-network attributes;

inter-annual variation is probably 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 realized economical and environmental benefits of transgenic crops²⁸, 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 world²⁹. Our case study demonstrates that the changes in pitfall and Vortis sampled species abundance recorded in GMHT crops previously⁸ 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 abundances⁸ 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 organizational 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 and opportunity 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 on 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 genetically modified crop variety or a new pesticide formulation. While the collection and analysis of data will probably become easier, for example, through the use of environmental DNA¹¹, 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 diversity³¹, higher order interactions³² and landscape³³ on agro-ecosystem functioning when viewed through the lens of ecological networks³⁴. 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

FSE. The FSE¹⁵ was a three-year study involving the analysis of the effects of GMHT crops to the farmland biodiversity across the United Kingdom, and the details of farmland selection and crop field design are described more fully elsewhere³⁵. To summarize, a split-field design was used in 64 beet, 57 maize, 65 spring-sown oilseed rape and 65 winter-sown oilseed rape 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 half³⁵. 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 (for example, body size and feeding type) were used to generate hypotheses in the form of trophic relationships between species (that is, food webs) using a logic-based machine learning approach called abductive/inductive logic programming 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}. On the basis of 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 abductive inductive logic programming 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; for example, conventional beet or GMHT maize and so on. We then applied the Bray–Curtis index³⁹, 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 disturbance²⁷. We applied complex network analysis to characterize 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 that are well interconnected with each other. We hypothesized that food webs in this study also exhibit this substructural property and applied a profiling technique²³ 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 (that is, $k_{r^*}^+ > k_r^+$ 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 coefficient⁴³, 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 $r(r-1)/2$ 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 disturbance⁴⁴. 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 collapsed²⁷. First, 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 $\sigma = 0.076$). Second, 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 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 least significant difference post hoc test to identify the contributing factors.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The raw FSE data are free from intellectual property rights. The data can be requested by enquiry to the Environmental Information Data Centre of the Centre for Ecology and Hydrology (<http://eidc.ceh.ac.uk/contact>). Archived information about the FSEs are available from the National Archives of The Government of the United Kingdom (<http://webarchive.nationalarchives.gov.uk/20080306073937/http://www.defra.gov.uk/environment/gm/fse/>).

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Author contributions

A.M. and D.A.B. designed the research. D.A.B. and A.T.-N. contributed materials and datasets. X.L. implemented the analysis. X.L. and C.G. analysed the data. A.M., X.L., C.G., A.R., G.W. and D.A.B. discussed the results. A.M. and D.A.B. led the paper writing with input from all authors.

Competing interests

A.R. is employed by Syngenta, which develops and markets genetically modified seed products.

Additional information

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Reporting Summary

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When statistical analyses are reported, confirm that the following items are present in the relevant location (e.g. figure legend, table legend, main text, or Methods section).

n/a Confirmed

- ☐ ☒ The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
- ☐ ☒ An indication of whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
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Only common tests should be described solely by name; describe more complex techniques in the Methods section.
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- ☐ ☒ A full description of the statistics including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- ☐ ☒ For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
Give P values as exact values whenever suitable.
- ☒ ☐ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- ☒ ☐ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- ☒ ☐ Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated
- ☒ ☐ Clearly defined error bars
State explicitly what error bars represent (e.g. SD, SE, CI)

Our web collection on [statistics for biologists](#) may be useful.

Software and code

Policy information about [availability of computer code](#)

Data collection

The data were collected as part of a large scale analysis of the effects of Genetically Modified, herbicide-tolerant (GMHT) crops in the UK. These data were published and peer reviewed as part of a number of papers in the period 2003-2006. A special issue of Philosophical Transactions of the Royal Society (Issue 358, 2003) collated much of the work and description of the data.

Data analysis

The data analysis conducted in this paper was done using open source statistical tools and published methods, as described in the text.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research [guidelines for submitting code & software](#) for further information.

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- A list of figures that have associated raw data
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A data and materials statement is provided in the manuscript.

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☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The data come from a 256 field trial of Genetically Modified, herbicide-tolerant (GMHT) crops in the UK (see Philosophical Transactions of the Royal Society (Issue 358, 2003) and Bohan et al. (2005) Proc. R. Soc. B 272, 463–474.). The trial was called the Farm Scale Evaluations of GMHT crops and made UK and worldwide headlines during the period 2000 - 2005. The FSEs is one of the largest agricultural experiments of management effects on biodiversity ever to be conducted. Each field was split in half (half-field design), with a conventional and GMHT variety of the same crop assigned to each half. 4 crops were tested (winter sown oilseed rape, spring oilseed rape, beet and maize). The data analysed were year total data.
Research sample	The data analysed came from the vortis suction sampling protocol for surface active invertebrates. The vortis protocol was one of a number of sampling protocols for agricultural biodiversity used during the FSEs.
Sampling strategy	We selected the vortis data because it proved, in post-hoc power analyses of the power of the FSE experiment, to be one of the most sensitive protocols. Power analyses published in Clark et al. (2006). Proc. R. Soc. B 273, 237–243.
Data collection	The vortis data were collected over a 3-agricultural year period from 2000 to 2005. Each field was followed for one agricultural year during this period, with approximately 1/3 of the 256 field sites being sampled at any one time. The large number of fields was split between research teams from three UK institutes (CEH, Rothamsted and SCRI). Please see Perry et al. (2003) Journal of Applied Ecology 40, 17–31. for a full description.
Timing and spatial scale	The data were year-total data.
Data exclusions	No vortis data were excluded.
Reproducibility	Reproducibility was analysed in the power analyses of the FSE, published as Clark et al. (2006). Proc. R. Soc. B 273, 237–243.
Randomization	Full randomization procedure for the trial were followed, with allocation of crops to field, and varieties to field halves following a completely (double blind) procedure as described in Perry et al. (2003) J. Appl. Ecol. 40, 17–31.
Blinding	All farmers involved in the study were initially unaware of which crop variety was allocated to each half of each field. All data were also anonymised to protect the farmers during this 'politically-charged' field experiment.
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

Field work, collection and transport

Field conditions	The field conditions were those of any large-scale agricultural field experiment. Field protocols had specific requirements for being conducted (temperature, rainfall, etc. see Philosophical Transactions of the Royal Society (Issue 358, 2003) for descriptions).
Location	256 fields across the UK (see Philosophical Transactions of the Royal Society (Issue 358, 2003) and Bohan et al. (2005) Proc. R. Soc. B 272, 463–474. for maps)
Access and import/export	All field sites were driven to. Fields were divided up into 24 sampling transects and these were visited by field sample operators on foot. Due to the 'political' nature of GMHT crops at the time, no crop plant material was removed from the field. Only samples of weeds and invertebrates, necessary for laboratory processing and identification, were removed and taken back to the laboratory.
Disturbance	The experimental design contained a protocol that assessed the impact of the sampling on the field. Any field positions that were considered to be too damaged to be useful or that had been lost due to outside activity (animals removing pitfall traps or the activity of anti-GM protesters, for example) were removed. Agriculture is a highly disturbed system and the long term effects of our activities were, in real terms, minimal.

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Unique biological materials
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants

Methods

n/a	Involved in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging