

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

2

3 Athen Ma¹, Xueke Lu^{1,2}, Clare Gray^{3,4}, Alan Raybould⁵, Alireza Tamaddoni-Nezhad^{6,7}, Guy Woodward⁴ and

4 David A. Bohan^{8*}

5

6 1. Queen Mary University of London, School of Electronic Engineering and Computer Science, Mile
7 End Road, London, E1 4NS, UK.

8 Email: athen.ma@qmul.ac.uk, xueke.lu@qmul.ac.uk

9 2. School of Engineering, University of Warwick, Library Road, Coventry, CV4 7AL, UK.

10 3. Queen Mary University of London, School of Biological and Chemical Sciences, Mile End Road,
11 London, E1 4NS, UK.

12 4. Department of Life Sciences, Silwood Park Campus, Imperial College London,
13 Ascot, Berkshire, SL5 7PY, UK.

14 Email: c.gray@imperial.ac.uk, guy.woodward@imperial.ac.uk

15 5. Syngenta Crop Protection AG., Schwarzwaldallee 215, CH-4058 Basel, Switzerland

16 Email: alan.raybould@syngenta.com

17 6. Department of Computer Science, University of Surrey, Guildford, Surrey, GU2 7XH, UK.

18 Email: a.tamaddoni-nezhad@surrey.ac.uk

19 7. Department of Computing, Imperial College London, 180 Queen's Gate, London, SW7 2BZ, UK.

20 8. Agroécologie, AgroSup Dijon, INRA, Univ. Bourgogne, Univ. Bourgogne Franche-Comté, F-21000
21 Dijon, France.

22 Email: david.bohan@inra.fr

23 * Corresponding author

24

25 **ABSTRACT**

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

41

42 **INTRODUCTION**

43 Developing management that conserves biodiversity whilst delivering the services we need from ecosystems
44 without introducing further harm is a pressing issue for the future of human societies^{1,2,3}. The demand for
45 sustainable food security and ecosystem services⁴ in the face of global change and biodiversity loss due to
46 current farming regimes, means new agricultural management practices¹ will be needed, based on sound
47 ecological understanding⁵. In agro-ecosystems, assessment of new practices concentrates primarily on risks to
48 biodiversity, and therefore aims to evaluate whether a novel management has an adverse effect on the
49 abundance and diversity⁶ of individual species or taxa against the noisy backdrop of natural variation.
50 However, if our aim is to manage agro-ecosystems for optimum delivery of ecosystem services, such a focus
51 may be too narrow⁷. Not only does this approach tend to disregard benefits of the new management to crop
52 yield and quality, but also, and more importantly for our purposes here, it may consider any change in

53 biodiversity as posing unacceptable risk⁸. Such conservatism in risk assessment stems in large part from a lack
54 of universal methods to evaluate the importance of structural and functional effects that changes in biodiversity
55 can be triggered via indirect effects that ripple through networks of interacting species. Moreover, many studies
56 suffer from a lack of replication⁹, leading to incomplete or inaccurate estimations of potential ecological risks⁵.

57

58 Ecological network approaches have been advocated as part of the next generation of biomonitoring tools^{10,11}
59 because they can capture the underlying functioning and dynamics emerging from complex species
60 interactions¹², whereas the traditional evaluation methods that focus on a few taxa can mask these higher-level
61 and often indirect synergistic or compensatory effects¹³. By elucidating the wider system, network approaches
62 could open the way to improving productivity while safeguarding biodiversity and ecosystem services in
63 agriculture via better decision-making based on more holistic, structural assessments. To date the low number
64 of highly resolved ecological networks has impeded their application in real-world agro-ecosystems. The recent
65 emergence of machine learning and molecular biological techniques provides new methodologies for
66 constructing large-scale replicated networks^{11,14}, although system-level responses to change remain mostly
67 unexplored.

68

69 Here we perform a large-scale assessment on agro-ecosystem responses by analysing a case study of 502
70 replicated food webs, from fields of the Farm Scale Evaluations (FSE) of genetically modified, herbicide-
71 tolerant (GMHT) crops¹⁵ (Methods and Supplementary Methods 1). The case study data-set is of in-field Vortis
72 suction and Pitfall sampled invertebrates from 251 fields of four widely grown crops, in a split-field design in
73 which conventional and GMHT varieties were grown alongside one another. From each half of the split-field,
74 we constructed a food web of species trophic relationships (Methods and Supplementary Methods 2).

75 Switching crops commonly causes biodiversity change in farmland¹⁶ but it is widely accepted as part of
76 traditional crop rotations, whereas the adoption of GMHT represents an alternative form of (future)
77 management. Previous FSE analyses have assessed farming biodiversity by focusing on species-specific
78 measures^{15,17}, such as changes in invertebrate populations indirectly driven by herbicide management of weed
79 plants, which can be sensitive to the inherent noise or the contingency of responses^{13,18} and functional traits¹⁹.

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

82

83 **RESULTS & DISCUSSION**

84 The dominant first-order effect was crop type (Fig. 1a, b, Supplementary Fig. 1 and Supplementary Table 1),
85 with a common suite of interconnected species evident in most field-sites, including typical farmland taxa such
86 as the carabids, *Pterostichus melanarius*, the detritivore collembolans of the Entomobryidae and Isotomidae,
87 and the linyphiid spider, *Lepthyphantes tenuis* (*Tenuiphantes tenuis*). Species dissimilarity (diversity) was high
88 among crop types, but noticeably lower when conventional crops were compared with their GMHT
89 counterparts (Fig. 1c) reflecting the greater differences of environmental conditions provided to invertebrate
90 species in the different crops⁸. The food webs of a given crop variety (e.g. conventional beet or GMHT maize)
91 varied greatly in size among sites; however, the conventional and GMHT webs always remained highly
92 correlated within sites (Supplementary Fig. 2).

93

94 Species turnover can significantly alter food web structure and dynamics, particularly where incoming and
95 outgoing nodes have markedly different links due to variation in their diet or consumers²⁰. A commonly used
96 structural metric of web complexity, connectance, was unchanged by crop type, but was significantly greater
97 under GMHT (Nested ANOVA $F_{4,247} = 2.79$, $P = 0.023$; Supplementary Table 2), which appears to be due to an
98 increase in links in the GMHT to the Collembola. Network theory suggests that higher levels of structural
99 complexity can confer food web stability, if most interactions are relatively weak²¹, and there is growing
100 evidence to support this in ecological networks²². However, such crude whole-network metrics can be relatively
101 insensitive to important but more subtle changes that may arise within the web, and newer substructural
102 measures can provide deeper insights here²⁰. For instance, cores are a cohesive substructure of highly
103 connected nodes that are said to govern the dynamics and functioning of complex systems, and their densely
104 intertwined pathways can provide redundancy to buffer external perturbations and maintain food web
105 robustness^{20,23}. We extracted the core properties²⁰ of the webs to evaluate whether network substructures
106 responded to farming regime. All the 502 food webs possessed cores surrounded by loosely connected
107 peripheral species (Supplementary Fig. 3), revealing a previously unknown but recurrent core-motif

108 (community) of species in agro-ecosystems that could be key for driving ecosystem properties²⁴. Crop type
109 resulted in significant variation in species composition in the substructures, and especially for peripheral
110 species (Fig. 2a, b). Substructuring, both in terms of organisation and composition, appeared to be largely
111 unaffected by GMHT management (Fig. 2c, d), again suggesting negligible impacts at these higher
112 organisational levels. In particular, the conventional and their GMHT counterpart webs shared significant
113 numbers of core and periphery species, with the species in the cores tending to be those that were common
114 across sites (Fig. 2c, d, Supplementary Fig. 4), such as the *Isotomidae* collembola.

115
116 Relatively large cores were observed across all the food webs, accounting for 65-71% of total species richness
117 on average (Supplementary Table 3), and these findings are similar to that observed in aquatic ecosystems
118 when comparing natural networks with others²⁰. The core size was strongly affected by crop type (Nested
119 ANOVA $F_{3,247} = 4.87$, $P = 0.002$; Supplementary Table 2), but was unchanged by GMHT management (Nested
120 ANOVA $F_{4,247} = 0.98$, $P = 0.416$; Supplementary Table 2). The link density within the core, gauged by the rich-
121 club coefficient²⁰, varied significantly among crop types (Nested ANOVA $F_{3,247} = 6.80$, $P < 0.001$;
122 Supplementary Table 2), but was again unaltered by GMHT management (Supplementary Fig. 5; Nested
123 ANOVA $F_{4,247} = 1.04$, $P = 0.386$; Supplementary Table 2). Changes in core size and core link density, here
124 induced by the crop type, are common network responses to external disturbance²⁵ (e.g. a stressor can reduce
125 core size which in turn results in lesser number of alternative paths within a food web for exchanges of energy
126 fluxes) which can potentially impact network redundancy²⁶ and robustness.

127
128 Altering agricultural practice could reshape the taxonomic and network properties of ecosystems and their
129 response to further external disturbance, such as biodiversity loss caused by current intensive agricultural
130 management⁵. To assess food web robustness, we applied two simple but common simulated scenarios of
131 species loss: random versus a risk scenario of targeted high-degree node removal, with the former representing
132 a “null model” and the latter mimicking the supposed ‘worst-case’ loss of highly connected keystone species²⁷
133 (Methods). The major differences were once again manifested between crop types, especially under targeted
134 removal (Nested ANOVA $F_{3,247} = 2.93$, $P = 0.034$, Supplementary Table 2). These findings illustrate how crop
135 type determines network properties that can potentially compromise the overall structural integrity and the

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

139

140 Our large-scale evaluation revealed network-level responses of GMHT crops are remarkably similar in their
141 composition, structure and responses to simulated trajectories of species removals, to their conventional
142 counterparts (Fig. 3). This suggests that previously recorded changes in taxa traits⁸ may be compensated for at
143 these higher organisational levels, due to prevalent trophic redundancy. Cultivating crops in rotational
144 sequences is integral to farming and we found that crop type was by far the dominant driver of differences in
145 web structure and robustness, across several organisational levels, ranging from substructural to whole-network
146 attributes; inter-annual variation is likely greater than differences between conventional and GMHT. This
147 demonstrates how traditional autecological analysis, which treats species as fixed taxonomic identities with
148 defined traits provides only a partial view of the potential ecological consequences of a change in management.
149 Despite the realised economical and environmental benefits of transgenic crops²⁸, their planting continues to
150 raise controversy in terms of perceived ecological and environmental risk, and this has restricted their adoption
151 in some parts of the world²⁹. Our case study demonstrates that the changes in pitfall and Vortis sampled species
152 abundance recorded in GMHT crops previously⁸ would have been less likely to be interpreted as a systemic and
153 potentially critical risk to the agricultural ecosystem if network-based approaches had been included from the
154 outset. The food web variation due to the GMHT could also have been set within the natural variation of the
155 conventional crops currently accepted in UK farmland. This case study does not, however, examine all the taxa
156 that exist in the FSE data (Supplementary Methods 1), notably not evaluating the effects of GM herbicide
157 management on networks of pollinators, which are of considerable interest worldwide. Reconstructing
158 networks for these other taxa from the FSE would test whether observed changes in species-specific
159 abundances⁸ translate to changes in network structure and ecosystem change and might modify the conclusions
160 of this case study.

161

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

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

174

175 The practicalities of using network analysis in decision-making about agricultural practices need careful
176 consideration. Using current methods, a programme the size of the FSE would be impractical for decision-
177 making about the use of individual products, such as a new GM crop variety or a new pesticide formulation.
178 While the collection and analysis of data will likely become easier, for example through the use of eDNA¹¹, the
179 size and duration of the experiments may prove too much for pre-market product regulation. We envisage three
180 scenarios where network analysis may be valuable. First, FSE-like experiments could be useful in decision-
181 making over the introduction of a new management technique or class of products that will be used extensively;
182 the adoption of winter-sown cereals and GMHT crops are examples of such widespread changes. Second,
183 network analysis could be used as a risk management tool after the introduction of a new management regime;
184 for example, the regime could be introduced on a limited area and network analysis used to assess whether its
185 ecological effects are acceptable; in effect, limited commercial use of a method would act like an FSE. Finally,
186 network analysis could be used to check the cumulative effects of products under current regulations and used
187 to test whether risk-assessment of species effects predict the resilience of ecosystem-service delivery by agro-
188 ecosystems. These analyses could contribute to debates about the roles of species diversity³¹, higher order
189 interactions³² and landscape³³ on agro-ecosystem functioning when viewed through the lens of ecological
190 networks³⁴. Results of such analyses could help to improve the design of “low-tier” laboratory studies and build

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

193

194 **METHODS**

195 **Farm Scale Evaluations (FSE).** The FSE¹⁵ was a three-year study involving the analysis of the effects of
196 GMHT crops to the farmland biodiversity across the UK, and the details of farmland selection and crop field
197 design are described more fully elsewhere³⁵. To summarise, a split-field design was used in 64 beet (B), 57
198 maize (M), 65 spring-sown oilseed rape (SR) and 65 winter-sown oilseed rape (WR) sites (Supplementary
199 Methods 1). Each crop field was split approximately in half and a conventional and GMHT variety of one of
200 the crops assigned randomly to each half^{15,35}. Species were sampled using Vortis suction and pitfall sampling,
201 and taxa identity and abundance information were recorded within the field across all the sites.

202

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

213

214 **Impacts of agricultural practice on food web size.** We evaluated the differences in the taxonomic
215 composition among crop types and management varieties by referring to their aggregated compositional webs,
216 which takes both the species and their frequency of appearance across all split fields into account. A total of
217 eight aggregated webs were obtained, e.g. conventional beet or GMHT maize, etc. We then applied the Bray-
218 Curtis index³⁹, b , to quantify the compositional similarity between two aggregated webs with reference to the

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

222

223 **Impacts of agricultural practice on food web structure.** We measured directed connectance of individual
224 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,
225 which is a common measure of food web complexity, reflecting its robustness in response to external
226 disturbance²⁷. We applied complex network analysis to characterise the substructural properties of all the
227 individual food webs. A network core refers to a cohesive substructure^{20,40} that consists of high degree (highly
228 connected) species which are well interconnected with each other. We hypothesized that food webs in this
229 study also exhibit this substructural property and applied a profiling technique²³ to define the cores in
230 individual food webs. Nodes were ordered in descending order of their degree. A node with a rank r has degree
231 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
232 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
233 $r > r^*$), indicating a change in the interconnectedness among high degree nodes. To compare the species
234 composition in the web cores between crop types and management, here again, we aggregated all the core
235 species and their frequency found in the cores across all spilt-fields and quantified the overall similarity using
236 the Bray-Curtis index. We repeated this analysis for the peripheral species composition.

237

238 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
239 number of species. This core property indicates a system's state: a large core is associated with a greater level
240 of redundancy within a system, which can mitigate the effect of external disturbance. On the other hand, stress
241 in a system is often manifested as a core of reduced size^{25,41,42}. We measured the density of links within the core
242 by calculating the rich-club coefficient⁴³, ϕ_r , which is given by:

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

243 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
244 of possible links among these nodes. The connectivity of a core is given by $\phi_{r,*}$ whereby a fully connected core
245 has a value of $\phi_{r,*} = 1$ and a fully disconnected core gives $\phi_{r,*} = 0$.

246

247 **Impacts of agricultural practice on food web robustness.** The architecture of food webs governs their
248 robustness and underpins their response to external disturbance⁴⁴. We studied the potential effect of
249 compositional, structural and substructural changes on network robustness using two simple but common
250 species removal scenarios, with no network link rewiring and evaluated the rate at which the network
251 collapsed²⁷. Firstly, species were removed at random at each simulation step, and the total species extinction is
252 the sum of primary loss and secondary loss as a result of species isolation from resource. We measured the
253 robustness for each web by recording the proportion of primary species loss resulting in a total extinction
254 (primary and secondary) of 50% of the species^{27,45}. For each food web, we ran the random removal simulation
255 for 100 times and results were averaged (within a standard deviation $\sigma = 0.076$). Secondly, species were
256 removed sequentially in descending order of degree to simulate the worst-case of loss of the most connected
257 taxa. When a node was removed from a food web, the degrees among the rest of the nodes were also altered,
258 and therefore, we re-calculated the degree order after each node removal. Again, we measured robustness as the
259 amount of primary taxa loss in order to generate a total of 50% species extinction.

260

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

269

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

275
276 **Supplementary Information** is linked to the online version of the paper at www.nature.com/nature.

277
278 **Acknowledgements** We thank John Bigham, Peter Curtis, Pavel Kratina, Ben Parker and Rosemary Bailey for
279 their comments and discussion. X.L. and C.G. were supported by Queen Mary University of London. X.L. was
280 additionally supported by the Chinese Scholarship Council and C.G. was additionally supported by the
281 Freshwater Biological Association. D.B. would acknowledge the support of the FACCE SURPLUS PREAR
282 and ANR (ANR-17-CE32-011) NGB projects.

283
284 **Author contributions** A.M. and D.B. designed the research. D.B. and A.T.N. contributed materials and
285 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
286 D.B. discussed the results. A.M. and D.B. led the paper writing with input from all authors.

287
288 **Competing Interests** The authors declare the following competing interests: A.R. is employed by Syngenta,
289 which develops and markets GM seed products.

290
291 **REFERENCES**

- 292 1. Tilman, D. *et al.* Global food demand and the sustainable intensification of agriculture. *Proc. Natl. Acad.*
293 *Sci.* **108**, 20260–20264 (2011).
- 294 2. Flohre, A. *et al.* Agricultural intensification and biodiversity partitioning in European landscapes
295 comparing plants, carabids, and birds. *Ecol. Appl.* **21**, 1772–1781 (2011).
- 296 3. Rockström, J. *et al.* A safe operating space for humanity. *Nature* **461**, 472–475 (2009).
- 297 4. Geiger, F. *et al.* Persistent negative effects of pesticides on biodiversity and biological control potential
298 on European farmland. *Basic Appl. Ecol.* **11**, 97–105 (2010).
- 299 5. Butler, S. J. *et al.* Farmland Biodiversity and the Footprint of Agriculture. *Science* **315**, 381–384 (2007).
- 300 6. Foley, J. A. *et al.* Solutions for a cultivated planet. *Nature* **478**, 337–342 (2011).

- 301 7. Firbank, L. G. *et al.* Assessing the impacts of agricultural intensification on biodiversity: a British
302 perspective. *Philos. Trans. R. Soc. B Biol. Sci.* **363**, 777–787 (2008).
- 303 8. Brooks, D. R. *et al.* The Implications of Genetically Modified Herbicide-Tolerant Crops for UK
304 Farmland Biodiversity : a Summary of the Results of the Farm Scale Evaluations Project. *Proc. Cultiv.*
305 *Genet. Modif. Crop. Eval. Ecol. Eff. Tokyo* 29–52 (2007).
- 306 9. Phalan, B. *et al.* Minimising the harm to biodiversity of producing more food globally. *Food Policy* **36**,
307 S62–S71 (2011).
- 308 10. Bohan, D. A. *et al.* Networking Our Way to Better Ecosystem Service Provision. *Trends Ecol. Evol.* **31**,
309 105–115 (2016).
- 310 11. Bohan, D. A. *et al.* Next-Generation Global Biomonitoring: Large-scale, Automated Reconstruction of
311 Ecological Networks. *Trends Ecol. Evol.* **32**, 477–487 (2017).
- 312 12. Thompson, R. M. *et al.* Food webs: reconciling the structure and function of biodiversity. *Trends Ecol.*
313 *Evol.* **27**, 689–697 (2012).
- 314 13. Hautier, Y. *et al.* Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature*
315 **508**, 521–525 (2014).
- 316 14. Bohan, D. A. *et al.* Automated Discovery of Food Webs from Ecological Data Using Logic-Based
317 Machine Learning. *PLoS One* **6**, e29028 (2011).
- 318 15. Firbank, L. G. *et al.* An introduction to the farm-scale evaluations of genetically modified herbicide-
319 tolerant crops. *J. Appl. Ecol.* **40**, 2–16 (2003).
- 320 16. Chamberlain, D. E. *et al.* Changes in the abundance of farmland birds in relation to the timing of
321 agricultural intensification in England and Wales. *J. Appl. Ecol.* **37**, 771–788 (2000).
- 322 17. Hawes, C. *et al.* Functional approaches for assessing plant and invertebrate abundance patterns in arable
323 systems. *Basic Appl. Ecol.* **10**, 34–42 (2009).
- 324 18. Haughton, A. J. *et al.* Invertebrate responses to the management of genetically modified herbicide-
325 tolerant and conventional spring crops. II. Within-field epigeal and aerial arthropods. *Philos. Trans. R.*
326 *Soc. Lond. B. Biol. Sci.* **358**, 1863–77 (2003).
- 327 19. Jordán, F. Keystone species and food webs. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **364**, 1733–1741
328 (2009).
- 329 20. Lu, X. *et al.* Drought rewires the cores of food webs. *Nat. Clim. Chang.* **6**, 875–878 (2016).
- 330 21. McCann, K. *et al.* Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798 (1998).
- 331 22. Jacquet, C. *et al.* No complexity–stability relationship in empirical ecosystems. *Nat. Commun.* **7**, 12573
332 (2016).
- 333 23. Ma, A. & Mondragón, R. J. Rich-Cores in Networks. *PLoS One* **10**, e0119678 (2015).
- 334 24. Gaston, K. J. Ecology. Valuing common species. *Science* **327**, 154–5 (2010).
- 335 25. Liu, Y.-Y. *et al.* Controllability of complex networks. *Nature* **473**, 167–73 (2011).
- 336 26. Brede, M. Coordinated and uncoordinated optimization of networks. *Phys. Rev. E* **81**, 66104 (2010).
- 337 27. Dunne, J. A. *et al.* Network structure and biodiversity loss in food webs: robustness increases with
338 connectance. *Ecol. Lett.* **5**, 558–567 (2002).
- 339 28. Brookes, G. & Barfoot, P. Environmental impacts of genetically modified (GM) crop use 1996–2015:
340 Impacts on pesticide use and carbon emissions. *GM Crops Food* **8**, 117–147 (2017).
- 341 29. Raybould, A. & Poppy, G. M. Commercializing genetically modified crops under EU regulations. *GM*
342 *Crops Food* **3**, 9–20 (2012).

- 343 30. Nations, U. The Millennium Development Goals Report. (2012).
- 344 31. Bairey, E., Kelsic, E. D. & Kishony, R. High-order species interactions shape ecosystem diversity. *Nat*
345 *Comms* **7**, 12285 (2016).
- 346 32. Levine, J. M., Bascompte, J., Adler, P. B. & Allesina, S. Beyond pairwise mechanisms of species
347 coexistence in complex communities. *Nature* **546**, 56–64 (2017).
- 348 33. Kaiser-Bunbury, C. N. & Bluthgen, N. Integrating network ecology with applied conservation: a
349 synthesis and guide to implementation. *AoB PLANTS* **7**, plv076 (2015).
- 350 34. Dormann, C. F., Fründ, J. & Schaefer, H. M. Identifying Causes of Patterns in Ecological Networks:
351 Opportunities and Limitations. *Annu. Rev. Ecol. Evol. Syst.* **48**, 559–584 (2017).
- 352 35. Rothery, P. *et al.* Design of the farm-scale evaluations of genetically modified herbicide-tolerant crops.
353 *Environmetrics* **14**, 711–717 (2003).
- 354 36. Tamaddoni-Nezhad, A. *et al.* Construction and Validation of Food Webs Using Logic-Based Machine
355 Learning and Text Mining. *Adv. Ecol. Res.* **49**, 225–289 (2013).
- 356 37. Tamaddoni-Nezhad, A. *et al.* *Machine Learning a Probabilistic Network of Ecological Interactions.*
357 *Proceedings of the 21st international conference on Inductive Logic Programming (ILP'11)* (Springer-
358 Verlag Berlin Heidelberg, 2012).
- 359 38. Davey, J. S. *et al.* Intraguild predation in winter wheat: prey choice by a common epigeal carabid
360 consuming spiders. *J. Appl. Ecol.* **50**, 271–279 (2013).
- 361 39. Bray, J. R. & Curtis, J. T. An Ordination of the Upland Forest Communities of Southern Wisconsin.
362 *Ecol. Monogr.* **27**, 325–349 (1957).
- 363 40. Borgatti, S. P. & Everett, M. G. Models of core/periphery structures. *Soc. Networks* **21**, 375–395 (1999).
- 364 41. Csermely, P. *et al.* Structure and dynamics of core/periphery networks. *J. Complex Networks* **1**, 93–123
365 (2013).
- 366 42. Csete, M. & Doyle, J. Bow ties, metabolism and disease. *Trends Biotechnol.* **22**, 446–50 (2004).
- 367 43. Zhou, S. & Mondragon, R. J. The Rich-Club Phenomenon in the Internet Topology. *IEEE Commun.*
368 *Lett.* **8**, 180–182 (2004).
- 369 44. Woodward, G. *et al.* Climate change impacts in multispecies systems: drought alters food web size
370 structure in a field experiment. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **367**, 2990–7 (2012).
- 371 45. Memmott, J. *et al.* Tolerance of pollination networks to species extinctions. *Proc. Biol. Sci.* **271**, 2605–
372 2611 (2004).

373

374 **Figure 1 | Variations in taxonomic composition.** Compositional trophic food webs of maize (shown as a
375 representative example of the four crop types). **a**, conventional; **b**, GMHT variety. The same species placement
376 is used in both cases. Node size and colour denote the proportion of times a species was found in the given crop
377 variety across all the sites. Nodes bounded by a dark edge are unique to their respective webs (i.e. were only
378 found in either conventional or GMHT spilt-fields). **c**, Comparisons of species dissimilarity between crop types
379 and management using the Bray-Curtis dissimilarity index. Colour denotes the degree of dissimilarity with $b =$
380 0 as the most similar and $b = 1$ as the most dissimilar.

381

382 **Figure 2 | Core/periphery substructures in food webs.** Comparisons of species composition between crop
383 types and GMHT management using the Bray-Curtis dissimilarity index. **a**, Core species; **b**, Peripheral species.
384 **c - d**, Pairwise compositional webs of maize (**c**, conventional; **d**, GMHT). The same species placement is used
385 in both cases. Node size denotes the proportion of times a species was found in the given crop variety across all
386 the sites. Colour denotes the gradient of core presence. Species that were always found in the core in both
387 conventional and GMHT are in the inner ring, and similarly, species that were consistently found in the
388 periphery in both conventional and GMHT are in the outer ring. Nodes that were found in both the core and the
389 periphery are in the middle ring. Nodes bounded by an edge denote absent species (unfilled) and species that
390 were unique to their respective web (filled).

391

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





