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A network perspective for sustainable agroecosystems

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Trends in Plant Science

A network perspective for nature-based agroecosystem management

--Manuscript Draft--

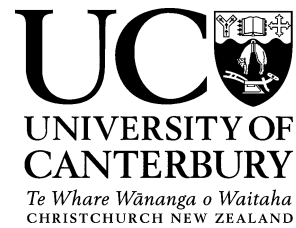
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Abstract:	Nature-based management promises to improve sustainable agroecosystem production, but its efficacy has been variable. Here we argue that nature-based agroecosystem management could be significantly improved by explicitly considering and manipulating the underlying networks of species interactions. A network perspective can link species interactions to ecosystem functioning and stability, identify influential species and interactions, and suggest optimal management approaches. Recent advances in predicting species' network roles from functional traits create opportunities for the direct manipulation of network architecture through targeted species additions or removals. Combined with improved understanding of the structure and dynamics of networks across interaction types (including social-ecological) and spatial and temporal scales, applying these tools to nature-based management can contribute to sustainable agroecosystems.
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22 November 2021

Dear Dr. Susanne Brink,

Thank you for commissioning our manuscript titled “*A network perspective for nature-based agroecosystem management*” as an Opinion article for Trends in Plant Science. We are pleased to now submit the complete manuscript for review.

As you know, plant-based agroecosystems support many of Nature’s Contributions to People and are increasingly challenged to meet sustainability goals in the face of global change. Increasing biodiversity through nature-based management (e.g. crop diversity, companion plantings, pollinator supplementation, biological control) presents a promising path towards sustainable agroecosystem production, but its efficacy to date has been variable. The reasons for this variable efficacy are not systematically understood, although the complex networks of species interactions that underpin nature-based management are likely a major source.

In this article, we argue that nature-based agroecosystem management can be significantly improved by considering the underlying networks of species interactions that affect and explain ecosystem functioning and stability, and which can be manipulated through the addition or removal of different species or genotypes. Tools now exist to predict species’ roles and interaction network structure based on functional traits, integrate multiple types of species interaction, and predict indirect effects across spatial and temporal scales. Thus, we have a growing understanding of the levers with which species interactions and ecosystem functioning can be manipulated, and applying these tools to nature-based management of agroecosystems could help address the urgent need for sustainable food production. We aim to stimulate research that will lead to improved design of nature-based management in agroecosystems, and believe that this manuscript will be of interest to agroecosystem ecology researchers, policy makers, and practitioners.

The manuscript was conceptualised during a two-day workshop over 13-14 April 2021. Should it ultimately be accepted, we would like to request permission to include all workshop participants as authors. Our team brings together leading experts with theoretical and applied knowledge in agroecology, interaction networks, biological invasions, below- and above-ground mutualisms, and functional trait ecology, and all authors made valuable contributions.

We thank you for your time and consideration of our manuscript.

Sincerely,

A handwritten signature in black ink, appearing to read 'Warwick Allen'.

Dr. Warwick Allen and co-authors

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1 **A network perspective for nature-based agroecosystem management**

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46 **Abstract**

47 Nature-based management promises to improve sustainable agroecosystem production, but its
48 efficacy has been variable. Here we argue that nature-based agroecosystem management could
49 be significantly improved by explicitly considering and manipulating the underlying networks
50 of species interactions. A network perspective can link species interactions to ecosystem
51 functioning and stability, identify influential species and interactions, and suggest optimal
52 management approaches. Recent advances in predicting species' network roles from functional
53 traits create opportunities for the direct manipulation of network architecture through targeted
54 species additions or removals. Combined with improved understanding of the structure and
55 dynamics of networks across interaction types (including social-ecological) and spatial and
56 temporal scales, applying these tools to nature-based management can contribute to sustainable
57 agroecosystems.

58

59 **Keywords:** ecological intensification; ecosystem functioning; functional traits; stability;
60 species interactions; sustainability

61 **The challenge of sustainable agroecosystems**

62 Over 40% of global land area has now been converted to **agroecosystems** (see Glossary
63 for definitions of keywords)¹, which supports many of **Nature's Contributions to People**
64 (**NCP**)². At the same time, the management of agroecosystems is increasingly required to
65 deliver **sustainability** goals while maintaining production, economic viability and social
66 license to operate. Agroecosystems are further faced with the effects of global change,
67 including pest, pathogen, and weed invasions³, pollinator declines⁴, and climate change⁵.

68 Increasing biodiversity through **nature-based management** presents a promising path
69 towards sustainable production in agroecosystems⁶. Approaches and policy goals include high
70 crop diversity (e.g. genetic diversity, intercropping, or crop rotation), restoration of non-crop
71 diversity with set-aside land and companion plantings (e.g. flower strips, beetle banks, in-field
72 trees, or conservation headlands), and targeted introductions of biological control agents,
73 pollinators, dung beetles, soil biota, and endophytes⁶. Yet simply manipulating diversity *per se*
74 is a blunt instrument that has seen mixed success as a proxy for increasing the range and effect
75 of species interactions^{7,8}. Instead, the power of any nature-based management approach relies
76 on our ability to effectively predict and manipulate underlying species interactions. However,
77 relatively few studies to date have explicitly considered the complex **species interaction**
78 **networks** that underpin nature-based management and their potential contributions to
79 **ecosystem functioning, stability**, and NCP provision.

80 In this article, we argue that the efficacy of nature-based agroecosystem management
81 can be significantly improved by considering and manipulating the underlying networks of
82 species interactions through the addition or removal of species or genotypes to promote direct
83 or indirect interactions that benefit the crop. We outline how a network perspective reveals the
84 functional roles of species (e.g. contributions to pollination, predation, resource acquisition)
85 and can mechanistically link network properties with ecosystem functioning and stability. We

86 then describe how recent advances in our understanding of species interaction networks have
87 opened a toolbox with which to better predict the impacts of global change and management,
88 and improve stakeholder communication within the broader social landscape.

89

90 **Network properties indicate ecosystem functioning and stability**

91 Agroecosystems comprise networks of **mutualistic** and **antagonistic** species
92 interactions (Fig. 1), with the importance of each type of network depending on agroecosystem
93 type and management. Species interaction networks can be studied from the perspective of
94 individual nodes (e.g. species, genotypes, or individuals), **motifs**, networks of one interaction
95 type, or **multi-interaction networks**⁹. The use of networks as a research tool has enhanced our
96 understanding of ecological and evolutionary processes that shape communities, how energy
97 flows through ecosystems, and the supply of NCP⁹⁻¹¹.

98 Agroecosystem functions (e.g. pollination, nutrient provisioning, biological control) are
99 mediated by both the diversity and strength of species interactions¹². For instance, ecosystem
100 functioning should increase when competing species partition interaction partners, described
101 in both communities and networks as '**complementarity**'¹³. Greater complementarity is
102 correlated with increased community-level pollination¹⁴ and natural enemy attack rates¹⁵ (Fig.
103 2A). Other network-level metrics could also be related to agroecosystem functioning, such as
104 high network **connectance**, which could reduce mutualist quality for crop species via
105 competition for mutualists or cross-pollination¹⁶ (but see Tylianakis and Morris 2017¹⁰ for
106 limitations to this metric). In antagonistic networks, the potential for indirect interactions like
107 **apparent competition** (e.g. pathogen spillover) should increase with high connectance and
108 low **modularity** (Fig. 2C). This may lead to adverse outcomes in agroecosystems where weeds,
109 wild plants, or companion plantings host generalist pathogens or pests that also affect the
110 crop¹⁷. Conversely, apparent competition between pest species can be beneficial, particularly

111 where crop and non-crop habitats hold similar communities¹⁸, but not all non-crop habitats
112 provide pest control services¹⁹. Thus, the effect of different network properties in
113 agroecosystems depends on the type of interaction and extent of species sharing.

114 Because species contribute unequally to ecosystem function and stability, metrics for
115 species within the network also link with functioning and productivity. For example, **generalist**
116 plants with high **centrality** in plant-pollinator networks attract a higher diversity and
117 abundance of pollinators²⁰, meaning that highly central crops produce more and heavier
118 seeds²¹. Moreover, these benefits are greatest when the generalist crop's interaction partners
119 are **specialists**, a characteristic structure of mutualistic networks known as **nestedness**²² (Fig.
120 2B). Invasive plant species can play disproportionate roles in pathogen and pest outbreaks,
121 often serving as **network hubs**²³. Managing plants with generalist pathogen interactions may
122 therefore prevent unwanted apparent competition with crops.

123 Ensuring stability of agroecosystems is another major challenge, especially in the face
124 of accelerating global change. Mutualistic networks with higher nestedness and connectance
125 tend to be more stable^{24,25} with greater **functional redundancy**, meaning species loss is less
126 likely to result in collapse, yielding high spatial and temporal consistency²². In antagonistic
127 networks, highly connected and less modular networks containing generalist pathogens and
128 herbivores can be less stable²⁴, but there is also evidence for stabilizing effects of connectance,
129 depending on the measure of stability (e.g. robustness, vulnerability, resilience)²⁶. Species may
130 also differ in their contributions to stability within a network. For example, species providing
131 NCP in salt marsh food webs did not generally play a stabilizing role, whereas species that
132 support NCP through their interactions were critical to the stability of both food webs and
133 NCP²⁷. Examining agroecosystem networks in a similar fashion could identify species that
134 contribute strongly to stability as well as multiple functions and NCP.

135 Finally, interaction network structure can also affect ecosystem resistance to or
136 recovery from invasions. Several theoretical and empirical studies have linked the success of
137 invading species to the interaction network structure of recipient ecosystems³, which can
138 predict invader impacts²⁸. For example, invasion success of an agricultural plant pathogen
139 (*Ralstonia solanacearum*) declined where rhizosphere bacteria competition networks had low
140 nestedness and high connectance²⁹. Generalist pathogens or plants that associate broadly with
141 mutualists may be more likely to invade networks³⁰. Furthermore, high modularity and low
142 connectance should limit the spread of invasion impacts through ecosystem networks³¹.

143

144 **Incorporating interaction networks into the design of agroecosystems**

145 Agroecosystems can be surprisingly diverse³², affording scope to manipulate
146 biodiversity through species additions or removals to optimise species interactions and benefit
147 sustainable production. Network manipulations could be informed by research that has
148 approached this challenge from the opposite direction - elucidating the mechanisms (including
149 species additions or losses) that underpinned observed changes in networks under changing
150 environmental conditions¹⁰. Thus, we argue that species' traits, the network type (including
151 social-ecological) being manipulated, and spatio-temporal scale can inform which species or
152 genotypes to add to or remove from agroecosystems to promote desired NCP.

153

154 *Linking functional traits with ecological interaction networks*

155 Species- and genotype-level traits, functional groups and community trait abundance
156 distributions can be manipulated to enhance functioning and stability in an agroecosystem
157 network³³. **Functional traits** reflect an organism's response to its environment (i.e. response
158 traits) and/or its contribution to an ecological function (i.e. effect traits)³⁴. Which species

159 prevail following agroecosystem intensification will depend on their response traits, while
160 functioning and NCP provision will depend on effect traits.

161 In addition to directly influencing ecosystem functioning and environmental responses,
162 species' traits are an important driver of interactions^{35,36} and their functional consequences³⁷,
163 such that species interactions provide an additional pathway through which traits influence
164 ecosystem functioning. Therefore, building response trait diversity and effect trait redundancy
165 into agroecosystem mutualist networks (e.g. via floral traits enhancing generalist pollinator
166 visits) may increase stability following environmental perturbations³⁷ because key interactions
167 are retained, even if species losses occur. The extent to which such knowledge can be used to
168 manipulate agroecosystem networks hinges on the predictive utility of traits. Tools exist to
169 predict both species' network roles and whole-network properties using functional traits^{35,38},
170 and to predict indirect effects of species, such as biological control agents, before their
171 introduction³⁹. However, interactions involving generalists and exotic species tend to be
172 predicted poorly by traits⁴⁰, and are instead better explained by species' relative abundances⁴¹.
173 Therefore, agroecosystem design should consider how both species' functional traits and
174 relative abundances influence interaction network structure.

175 Specialist species have the most distinct traits, and thereby contribute most to functional
176 diversity³⁶, suggesting that both functional diversity and interaction complementarity could be
177 maximised by introducing specialists. Since partner specialisation relates directly or indirectly
178 to many network structural properties (e.g. nestedness, connectance, modularity) and the
179 community assembly processes that generate them⁴², multiple aspects of agroecosystem
180 network structure can be modified through the introduction, retention, or removal of specialists
181 or generalists, which often have traits that are, respectively, far from or close to the community
182 average³⁶.

183

184 *Multi-interaction networks in agroecosystems*

185 The simultaneous consideration of multiple types of species interaction networks is
186 essential to maximise benefits of nature-based management by identifying synergies and trade-
187 offs between network types. For example, flower strips should increase pollination and pest
188 control, but could also create pest and pathogen reservoirs (Fig. 2C)¹⁷. These multi-interaction
189 impacts may be predicted by functional traits, like the floral area of candidate species for
190 companion plantings⁴³. Knowledge of multi-interaction networks could further improve these
191 predictions by considering traits and effects across a range of interaction types to select species
192 that optimise crop benefits and avoid trade-offs.

193 Research into the interplay between different network types has been growing rapidly⁴⁴⁻
194 ⁴⁷, including the development of analytical tools to unify multiple interaction networks into a
195 single framework^{48,49}. These approaches could be incorporated into agroecosystem
196 management. For example, a recent study that combined mutualistic and antagonistic networks
197 from Spanish olive (*Olea europaea*) farms found that low agrochemical use promoted
198 beneficial plant-pollinator and prey-predator/parasitoid motifs, whereas intensive agriculture
199 favoured generalist and intraguild predation interactions, which may inhibit agroecosystem
200 services⁵⁰. The same approach of dissecting multi-interaction networks into motifs could be
201 applied to examine the impacts of global change threats or nature-based management in
202 agroecosystems. Other benefits of a multi-interaction approach include the integration and
203 analysis of social-ecological networks (Box 1).

204 Species' multi-trophic effects should be carefully considered in agroecosystem design
205 because species can link co-occurring interaction networks of different types. For example, an
206 abundant generalist plant may act as a network hub and connector across multiple networks by
207 interacting with both generalist insect pollinators and generalist herbivore species⁴⁶. The
208 addition of generalist hub or connector species may promote agroecosystem stability and

209 function through the maintenance of a variety of interactions. However, Pocock et al. (2012)⁴⁴
210 found that while stability of individual agroecosystem networks varied in response to species
211 loss, effects did not propagate across the different networks. Thus, the potential to achieve net
212 benefits by manipulating subnetworks independently will depend on the extent to which a
213 species has a similar impact on all its interaction partners. Fortunately, plants that share
214 mutualists do not necessarily share herbivores⁴⁵, suggesting that interaction complementarity
215 could be optimised for beneficial interactions without exacerbating harmful ones (Fig. 2C).
216 Understanding species' network roles in a multitrophic context is therefore important for
217 identifying species with disproportionate effects on biodiversity, functioning, or NCP, thereby
218 underpinning new strategies towards stable and sustainable production in agroecosystems.

219

220 *Agroecosystem networks across spatial scales*

221 Nature-based management is often focused at the field scale, yet targeted species
222 manipulation could create spillover effects between habitats within a landscape. For example,
223 where hosts in neighbouring habitats share parasitoids, host abundance is coupled across spatial
224 boundaries via the shared parasitoids (apparent competition)¹⁸. The magnitude of spillover
225 effects on interaction networks depends partially on habitat permeability. Cross-habitat
226 pollinator movement, for example, can be altered by boundary effects, barrier effects⁵¹, and
227 dilution by adjacent land covers⁵². Designing landscapes that facilitate desirable and restrict
228 undesirable cross-network flows must account for spatial configuration of habitat patches⁵³.
229 Furthermore, describing interaction networks in neighbouring agroecosystems could help
230 identify habitat-connecting species⁴⁶, which are most likely to support stability⁵⁴. Future
231 studies may be able to use networks to identify organisms that disproportionately contribute to
232 bidirectional resource flow⁵⁵ between different crops or management types, and to evaluate the
233 feasibility of independent management of agroecosystems across the landscape.

234

235 *Evolution within agroecosystem interaction networks*

236 Evolution influences nature-based management in two key ways. First, pest or pathogen
237 impact can be exacerbated by their evolutionary responses to chemical⁵⁶ or biological⁵⁷ control.
238 However, evolutionary responses to a single pressure can be diluted or traded off when a
239 species experiences multiple pressures. Thus, natural enemies can delay the evolution of pest
240 resistance to Bt crops⁵⁸ and multiple parasitoid species can slow the evolution of host resistance
241 to parasitism⁵⁷ (Fig. 2D). In this sense, properties of interaction networks (e.g. natural enemy
242 redundancy) can have evolutionary impacts, alongside the ecological impacts discussed above.
243 Moreover, a species' population size influences its evolutionary potential, such that the impact
244 of enemies on pest population size influences the evolution of pest resistance to enemies. These
245 eco-evolutionary feedbacks can be manipulated through harvest management⁵⁹. Tools now
246 exist that can incorporate eco-evolutionary feedbacks into interaction network analysis^{60,61}, and
247 these adaptive network models may help to develop a predictive understanding of how species
248 manipulations affect agroecosystem network structures over evolutionary timescales.

249 Second, environmental changes can affect a large range of species interactions and
250 although crop plants typically are not evolving *in situ* themselves, their mutualists and enemies
251 both undergo natural selection in response to the environment. This selection can influence
252 interaction network structure⁶² and interactions with enemies can influence the fitness response
253 of plants⁶³ and pests⁶⁴ to environmental changes, such that network architecture can both
254 influence and respond to evolutionary processes. Maximising evolutionary plasticity of
255 beneficial species is therefore essential to accommodate ongoing ecosystem perturbations, both
256 biotic and abiotic. This could be manipulated by ensuring that any species introduced to the
257 agroecosystem (e.g. biological control agents) is sourced from diverse geographical and
258 ecoclimatic conditions.

259

260 **Concluding remarks and future perspectives**

261 Agroecosystems are made up of multiple, complex networks of species interactions,
262 with cross-network flows within habitats and across the wider landscape. Because
263 agroecosystems consist of relatively few crop species, network approaches may be most
264 impactful if they focus on species' roles within the network and motifs that include the focal
265 crop. For example, the introduction of specialists can improve complementarity, functioning
266 and some aspects of stability, whereas generalists will promote redundancy and stability across
267 multiple interaction networks and landscape-scale networks.

268 With the increasing availability of molecular data, and continued theoretical and
269 analytical advances, we now have the tools needed to apply a network perspective to nature-
270 based management of agroecosystems. For example, functional traits can predict species' roles
271 and their direct and indirect interactions, allowing for influential species to be identified and
272 added or removed from the agroecosystem. Furthermore, understanding how networks join
273 different interactions or habitats together can improve functioning and stability at multiple
274 spatial scales, and adaptive network models show promise to incorporate eco-evolutionary
275 changes. Future research should explore agroecosystem networks from plant to landscape
276 scales, integrating ecological and social sub-networks. This would serve to quantify the
277 impacts of nature-based management on agroecosystem interaction networks, clarify
278 mechanisms through which these impacts can be predicted and optimised, and parameterise
279 adaptive eco-evolutionary network models (see Outstanding Questions). Ultimately, applying
280 these tools can predict the short- and long-term impacts of intentional or accidental species
281 additions and removals (i.e. nature-based management) on ecosystem functioning, stability,
282 and NCP provision, from the plant to landscape scale.

283 **Glossary**

284 **Agroecosystem:** ecological systems modified to produce food, fibre, fuel and other products
285 for human consumption and processing (e.g. intensive and extensive pastures, orchards,
286 vineyards, forestry, etc.), and with strong interactions between ecological processes and
287 management.

288 **Antagonistic:** an interaction between two organisms that benefits one to the detriment of the
289 other (e.g. plant-herbivore, plant-pathogen and prey-enemy interactions).

290 **Apparent competition:** indirect negative interaction between two or more organisms which is
291 mediated by changes in the population or behaviour of shared natural enemies, including
292 pathogen spillover/spillback.

293 **Centrality:** a set of network metrics (e.g. closeness centrality and betweenness centrality) that
294 reflect the extent to which one node is directly connected to other nodes.

295 **Complementarity:** the degree to which nodes in a given network partition resources or
296 interaction partners.

297 **Connectance:** the proportion of possible links between nodes that are realised, which describes
298 the structural complexity of the interaction network.

299 **Ecosystem functioning:** the collective life activities of plants, animals, and microbes and their
300 effects on the biotic and abiotic processes that sustain an (agro)ecosystem.

301 **Functional redundancy:** when multiple species share similar ecological functions, such that
302 the loss of one species would not impact overall ecosystem functioning.

303 **Functional traits:** morpho-physio-phenological traits that determine species' effects on
304 processes and their responses to the environment.

305 **Generalist:** an organism that interacts with many others in the community often across a broad
306 taxonomic range.

307 **Modularity:** a network characteristic where interactions are primarily within subgroups (or
308 compartments) rather than across the broader network.

309 **Motifs:** recurrent patterns of interactions within and across networks.

310 **Multi-interaction network:** networks combining different species interaction types.

311 **Mutualistic:** an interaction between two organisms where both benefit (e.g. plant-pollinator,
312 plant-mycorrhiza, plant-rhizobia).

313 **Nestedness:** network characteristic where specialists tend to interact with generalists, while
314 generalists interact with both generalists and specialists.

315 **Network hub:** a generalist node with high centrality in the network.

316 **Nature-based management:** using specific components of biodiversity to complement or
317 replace artificial inputs and increase agricultural productivity (also known as ecological
318 intensification). Practices include increasing crop diversity, set-aside land and companion
319 plantings, active soil management, and biotic introductions.

320 **Nature's Contributions to People (NCP):** all the contributions, both positive and negative,
321 of living nature to quality of life for people. Beneficial contributions include food production,
322 climate mitigation, and nutrient cycling, whereas harmful contributions include zoonotic
323 disease transmission and pest and pathogen outbreaks.

324 **Specialist:** an organism that interacts with few other organisms in the community, often within
325 a restricted taxonomic range.

326 **Species interactions network:** a graphical representation of the biotic interactions in an
327 ecosystem, where nodes (e.g. species, genotypes, or individuals) are connected by links (e.g.
328 pairwise interactions) that can range from mutualistic to antagonistic.

329 **Stability:** the capacity to resist and recover from perturbation to provide temporal and spatial
330 constancy of agroecosystem outputs. We use this term in a broad sense to incorporate other
331 more specific terms such as vulnerability, robustness, and resilience.

332 **Sustainability:** the ability to maintain agroecosystem outputs while avoiding the depletion of
333 natural, social, and economic resources.

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469

470 **Box 1 References**

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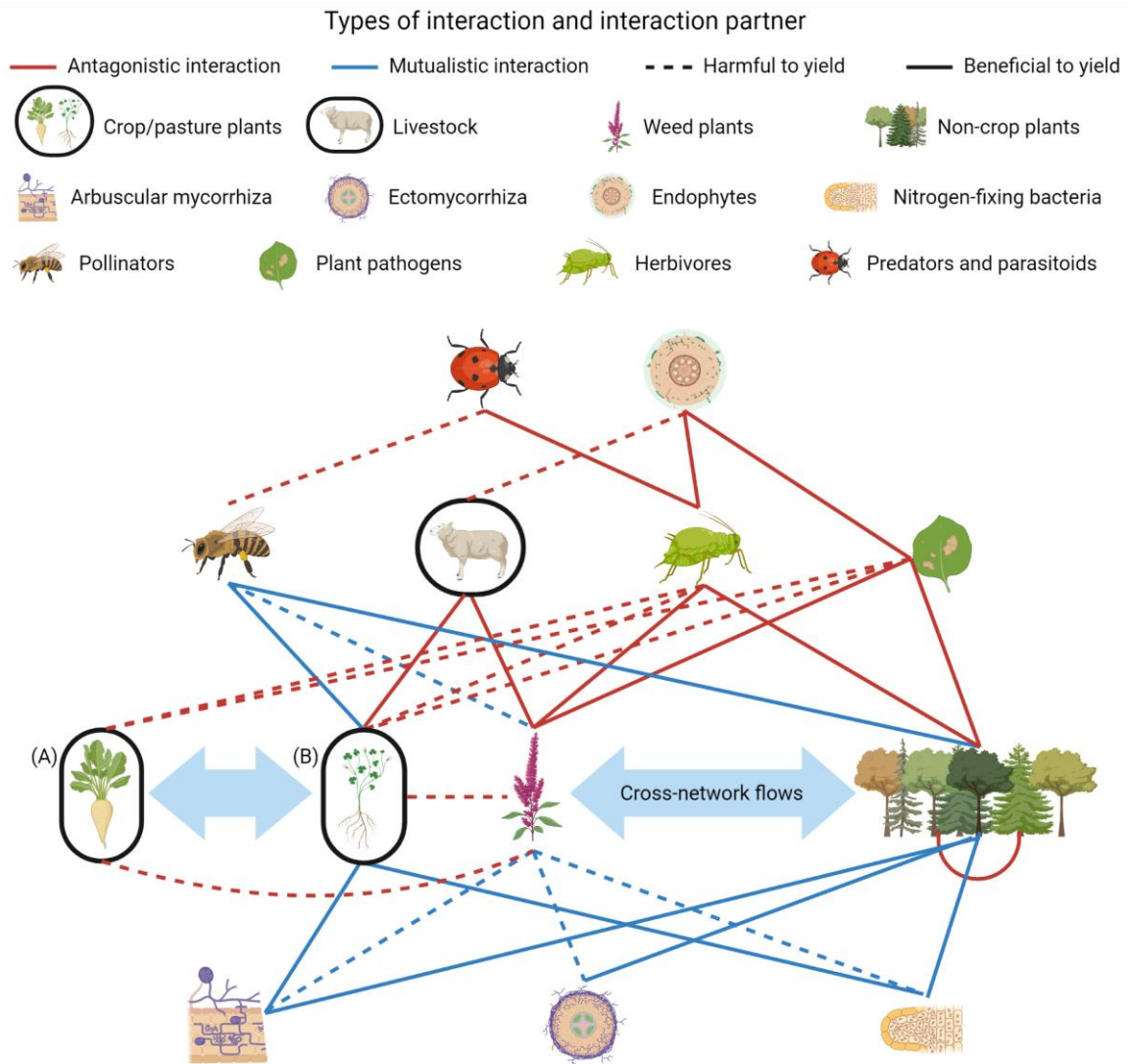
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489

490 **Figure 1. Generalised schematic of important species-interaction networks in different**

491 **types of agroecosystems and neighbouring habitat.** Networks shown include the interactions

492 of focal crop plants and/or livestock (highlighted with black outlines) with different types of

493 interaction partners (each here represented by a single characteristic species): weeds,

494 mycorrhizal fungi, N-fixing bacteria, pollinators, pathogens, and herbivores, as well as second-

495 tier interactions involving predators, parasitoids, and endophytes. Some of these interaction

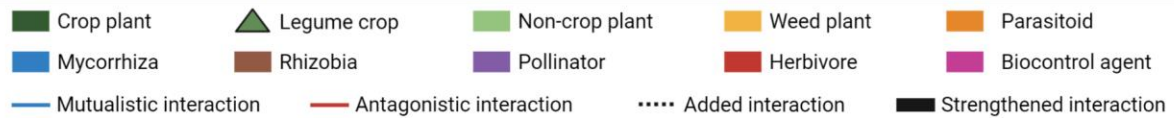
496 partners will be shared with networks in neighbouring habitats. Interactions shown represent

497 only a subset of the potential interactions that occur in agroecosystems (e.g. hyperparasitoids,

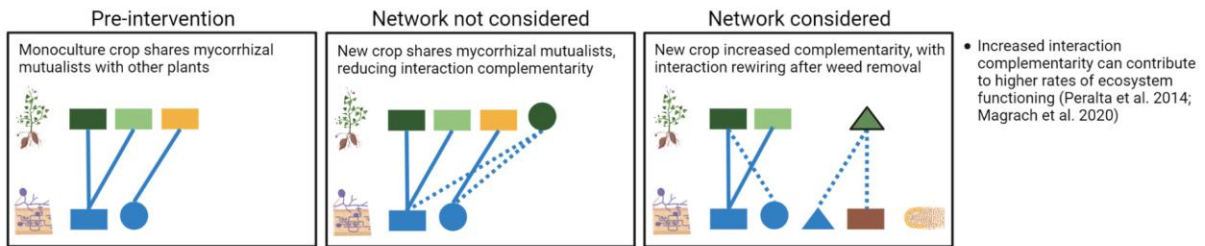
498 parasites, decomposers, and other soil biota have been excluded for simplicity). Also shown is

499 the potential for cross-network flows among habitat patches (blue arrows), the strength of

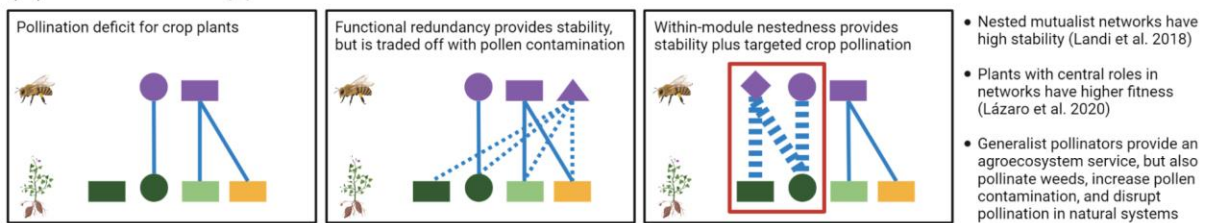
500 which depends on how species connect networks across habitat boundaries. Red lines represent
501 negative interactions (antagonism) and blue lines positive interactions (mutualism). Within
502 crop habitats, dashed and solid lines indicate interactions that are generally considered harmful
503 and beneficial to yield (crop or livestock), respectively. We selected two example
504 agroecosystems to demonstrate broad variation in network structure: (A) Beetroot (*Beta*
505 *vulgaris*) is a widely-grown annual crop that is non-mycorrhizal, largely wind-pollinated, and
506 susceptible to many pests and pathogens. (B) Grazing pastures that consist of many species
507 interactions, including biological control of pests and weeds, pollination, and other mutualisms.



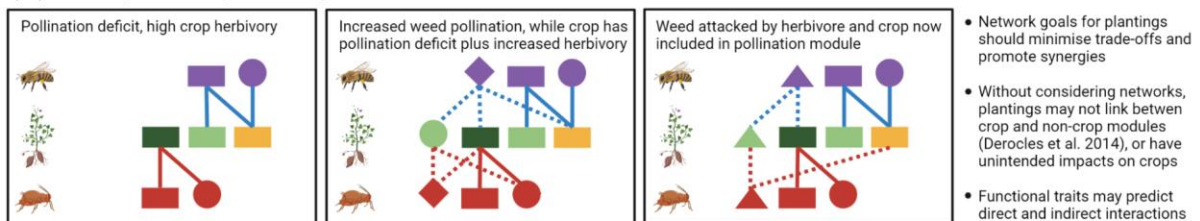
(A) Crop diversity and soil biota complementarity



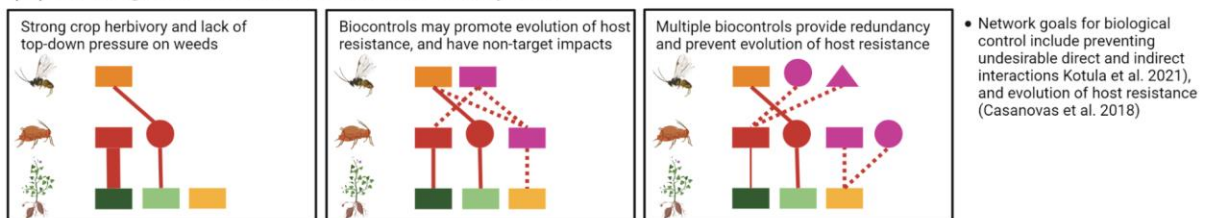
(B) Pollinator supplementation



(C) Companion planting



(D) Biological control of weeds and pests



508

509 **Figure 2. Hypothesised impacts of species additions and removals on simplified example**

510 **agroecosystem interaction networks.** Shown are examples of how knowledge of interaction

511 network structure could improve the efficacy of nature-based agroecosystem management. For

512 each management intervention, a hypothetical network is shown prior to management

513 intervention (left), after management that did not consider interaction networks (middle), and

514 after targeted changes to biodiversity based on knowledge of interaction networks, and where

515 functional traits may be used to predict interactions (right). Different symbol shapes represent

516 different species for each interaction partner. (A) Impact of increased crop diversity on the
517 complementarity of belowground plant-mutualist networks. Management of belowground
518 mutualist networks has the potential to improve sustainable production in agroecosystems,
519 although more research is needed to understand their importance and tractability. (B) Impact
520 of pollinator supplementation on the richness and strength of interactions in plant-pollinator
521 networks. The red box highlights the nested crop module of the broader plant-pollinator
522 network. (C) Impact of companion planting on pollinator-plant-herbivore networks. Depicted
523 is a trade-off for crop plants when plantings do not consider multi-interaction networks
524 (increased pollination but also herbivory), but a synergy (increased pollination but not
525 herbivory for crop plants, plus increased weed herbivory) when plantings consider the resident
526 network. (D) Introduction of biological control agents of weeds and crop pests into plant-
527 herbivore-parasitoid networks. Incorporating interaction redundancy of biological control
528 agents will increase stability of the service and minimise the evolution of host resistance.

529 **Box 1. Linking social networks with agroecosystems**

530 Network analyses can identify opportunities to enhance sustainable agroecosystem
531 production by selecting species for manipulation. However, one species that is rarely integrated
532 into agroecosystem networks is humans. This is surprising given that multiple community
533 groups, including farmers, industry, consumers, indigenous peoples, local communities,
534 policy-makers, and researchers, are responsible for creating and benefitting from
535 agroecosystems, applying management and receiving NCP⁶⁵. In many cases, communication
536 and collaboration among these groups are essential for successful implementation of nature-
537 based management⁶⁶. Therefore, a better understanding of the interactions within and between
538 these groups and their relationships with agroecosystems could inform policy that addresses
539 their multiple, and sometimes conflicting, values. The use of social-ecological network
540 analyses may facilitate progress in these areas⁶⁷.

541 First, social network analyses can be used to describe the degree to which institutions
542 are aligned with the structures and processes of the ecosystems they govern (institutional fit)⁶⁸.
543 Analysis of these institutional-level networks could identify conflicts or gaps in governance
544 that can be resolved to support the implementation of nature-based management. Second,
545 analysing social networks can be used to identify influential stakeholders and improve the
546 spread of information among land users. For example, one study found that the uptake of
547 rotational grazing by farmers in the United States depended upon strong linkages both within
548 social groups and between different types of stakeholder institutions⁶⁹. Another study of
549 farmers in Northern Spain found that those who used modern intensive irrigation dominated
550 the social network and were better able to control information flow within the community,
551 potentially jeopardising sustainable practices associated with more traditional farming
552 practices⁷⁰. Future studies that identify generalisable traits of influential stakeholders and other
553 important social network properties could improve uptake of nature-based management in

554 agroecosystems (see Outstanding Questions). Third, social networks could also prove valuable
555 at larger geographic scales, such as using international trade networks to quantify the flow of
556 NCP⁷¹ or to identify high-risk introduction pathways for invasive pest, pathogen and weed
557 species⁷². Finally, visualising ecological networks themselves can be an effective
558 communication tool to incentivise farmers to adopt nature-based management practices⁷³.
559 Taken together, we argue that integrating ecological and social networks can unify broader
560 community support, and promote the uptake and efficacy of biodiverse, multifunctional and
561 economically viable agroecosystem landscapes.

562 **Box 2. Practical recommendations for applying network principles to nature-based**
563 **agroecosystem management.**

564 In addition to future research priorities (see Outstanding Questions), we suggest a series
565 of practical steps to incorporate interaction network principles with nature-based management
566 in the field:

- 567 1) Identify the species or services that need to be promoted or controlled by measuring the
568 key NCPs that are targeted for improvement.
- 569 2) Focusing on these species, and the focal crop(s), characterise the existing species
570 networks, considering both the field and neighbouring habitats. As networks vary
571 substantially across crop types, environmental gradients, and within different
572 landscapes, this step will need to be done on locally representative fields. Interactions
573 could be observed or inferred through databases or eDNA, providing key information
574 for further interventions that can also be shared via local to global social networks (Box
575 1).
- 576 3) Use existing knowledge of species and their functional traits, including local and
577 indigenous knowledge, scientific studies and network models, to estimate how adding
578 or removing species will change network properties and the presence and strength of
579 direct and indirect interactions (motifs). Evaluate whether these changes are likely to
580 have a net positive or negative effect on the desired NCP. This can be done both by
581 predicting the specific interactions likely to be affected and by examining the change
582 in network properties or species' roles (e.g. connectance, complementarity, centrality).
583 Where possible, select species for manipulation which are least likely to have complex
584 indirect effects which will be hard to predict, for example by selecting specialist
585 biological control agents instead of generalists.

- 586 4) Evaluate which other management actions (e.g. synchrony of harvest timing, leaving
587 overwinter stubbles), additional to direct species addition or removal, are likely to result
588 in the desired species composition changes. Analysing the changes to indirect
589 interactions or multi-interaction networks can be used to screen for effective
590 management options.
- 591 5) After implementing management, re-assess the desired NCP and interaction network to
592 confirm the predicted effects, inform future management and improve our
593 understanding of interaction network manipulation as a management tool.

Highlights

- Nature-based management uses biodiversity and targeted biotic introductions to improve sustainable agroecosystem production, but results have been variable.
- A network perspective can improve the design and efficacy of nature-based agroecosystem management.
- Species interaction networks affect and explain ecosystem functioning and stability. Recent advances in network research provide tools for predicting species' roles and interaction network structure based on functional traits, integrating multiple types of species interaction, and predicting indirect effects across spatial and temporal scales.
- Applying these tools can help predict the impacts of intentional or accidental species additions and removals on ecosystem functioning and stability and contribute to sustainable agroecosystem production through nature-based management and in the face of global change.

Outstanding Questions

- *How does nature-based management affect agroecosystem interaction networks and their impacts on functioning, stability and productivity?* This question is central to enhancing nature-based management and will require detailed surveys and experiments to answer. Ideally, research will identify generalisable traits of species and social actors that optimise agroecosystem functioning and stability.
- *How do interactions among sub-networks affect agroecosystem functioning, stability, and productivity?* Enhancing nature-based management requires a systematic understanding of how networks and functioning link across interaction types, habitat patches, and eco-evolutionary time scales. Studies of agroecosystem networks have largely focused on bipartite above-ground interactions; future research should consider interactions across crop boundaries, seasons, trophic levels, and the above-belowground boundary.
- *What organism traits connect key functions of agroecosystem networks across habitats and confer functional stability?* Understanding whether functional traits (e.g. mobility, generalism) or abundance determine which species influence networks or cross-network interactions can identify key species for manipulating landscape-scale networks.
- *How does the spatial configuration of networks influence their combined functioning?* A systematic understanding of the structure and dynamics of landscape-scale interaction networks is needed, including non-additive effects of habitat patch arrangement. Landscapes are also the basic unit for social-ecological interactions, so understanding at this scale could improve uptake of nature-based management.

- *How does interaction network structure interact with eco-evolutionary feedbacks?*

Evolution is expected to alter networks and vice versa, but the frequency, timescale and impact of these effects is not understood. Adaptive network models can predict eco-evolutionary changes, but a major future challenge is to parameterise them with real-world data.

