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RESEARCH ARTICLE

Identifying plant mixes for multiple ecosystem service provision in agricultural systems using ecological networks

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Abstract

1. Managing agricultural environments in a way that maximises the provision of multiple ecosystem services is a significant challenge in the development of sustainable and secure food systems. Advances in network ecology provide a way forward, particularly in arable landscapes, as they incorporate mutualistic and antagonistic interactions associated with crop production.
2. Here, we present an approach to identify mixes of non-crop plant species that provide multiple ecosystem services while minimising disservices. Genetic algorithms were applied to the Norwood Farm ecological network—a comprehensive dataset of antagonistic and mutualistic species interactions on an organic farm in the United Kingdom. We aimed to show how network analyses can be used to select plants supporting a high diversity of insect pollinators and parasitoids of insect pests, but low diversity of herbivores. Further to this, we wanted to understand the trade-offs in ecosystem service provision associated with conventional management practices that focus on individual ecosystem services.
3. We show that multilayer network analyses can be used to identify mixes of plant species that maximise the species richness of pollinators and parasitoids (natural enemies of insect pests), while minimising the species richness of herbivores.
4. Trade-offs between ecosystem processes were apparent with several plant species associated with a high species richness of both positive (pollinators and parasitoids) and negative (herbivores) functional taxonomic groups. As a result, optimal plant species mixes for individual ecosystem services were different from the mix simultaneously maximising pollination and parasitism of pest insects, while minimising herbivory.
5. *Synthesis and applications*. Plant mixes designed solely for maximising pollinator species richness are not optimal for the provision of other ecosystem services and disservices (e.g. parasitism of insect pests and herbivory). The method presented here will allow for the design of management strategies that facilitate the provision of multiple ecosystem services. To this end, we provide a protocol for

practitioners to develop their own plant mixes suitable for farm-scale management. This avenue of predictive network ecology has the potential to enhance agricultural management, supporting high levels of biodiversity and food production by manipulating ecological networks in specific ways.

KEYWORDS
biocontrol, ecosystem services, network ecology, plants, pollinators, species interactions, sustainable agriculture

1 | INTRODUCTION

With an estimated doubling of global food demand by 2050, feeding an additional two billion people while using less environmentally damaging agricultural practices is a major challenge (Ehrlich & Harte, 2015). Developing effective methods to sustainably manage agricultural environments is therefore crucial (Landis, 2017). Current agricultural policy aims to use sustainable systems-based approaches (e.g. EU Common Agricultural Policy), moving away from the previous paradigm of production-focused systems which are heavily reliant on synthetic fertilisers and pesticides (Garnett et al., 2013). Sustainable management approaches focus strongly on biodiversity due to its relationship with beneficial ecological processes. For instance, biodiversity in agroecosystems is associated with pollination (Vanbergen & Initiative the Insect Pollinators, 2013), natural pest control (Derocles et al., 2014) and soil nutrient provision and turnover (Bodelier, 2011). These processes are typically studied in isolation, yet recent work has simultaneously assessed the pressures, impacts and responses of multiple ecosystem services in agricultural systems (Moss et al., 2021).

Although the response of biodiversity to agricultural management strategies has been the focus of research on sustainable agriculture (Šálek et al., 2018), beneficial ecological processes (ecosystem services; Zhang et al., 2007) are not simply a product of total species richness (Anderson et al., 2009). Across agricultural landscapes, the provision of ecosystem services emerges as a result of a complex series of interactions between species (including humans); within and between biological communities; and across both cropped fields and other natural and semi-natural habitats (Power, 2010). As such, ecological networks provide a framework for studying biodiversity–ecosystem functioning relationships in agroecosystems (Bohan et al., 2013). To harness the ecosystem services, as well as build more resilient agroecosystems, predictive methods from network theory are required to inform decision-making and management (Raimundo et al., 2018).

To date, few studies have attempted to use holistic network-based analyses to inform agricultural management. Instead, studies have tended to focus on describing bipartite networks at different scales (e.g. plant–pollinator and host–parasitoid across farms and landscapes; Bohan et al., 2013). As such, a fundamental challenge is to characterise and understand the link between ecosystem complexity and ecosystem service provision. Studies have made progress in understanding the complexity of ecosystems by developing methods that incorporate multiple interaction types found in the environment, for example both mutualistic and antagonistic species interactions (Fontaine et al., 2011). Such advances mean that it is now possible to simultaneously assess different interaction types, and their influence on ecosystem service provision within agricultural environments.

Plants form an integral component of ecological networks, providing important bottom-up effects that can alter both the nature and intensity of species interactions at higher trophic levels (Ebeling et al., 2018). The diversity and composition of plants alters ecosystem structure, including the abundance of herbivorous insects (Wan et al., 2019) and pollinators (Ebeling et al., 2008), the diversity of both predators and parasitoids (Schuldt et al., 2019) and the stability of associated food webs (Haddad et al., 2011). Furthermore, they are directly responsible for important ecological functions such as primary productivity (Wan et al., 2020). The central role of plants in ecosystems means that it is possible to use bottom-up approaches, such as managing plant species composition, to increase agricultural productivity and other ecosystem services (Isaacs et al., 2009; Storkey et al., 2015). In this sense, bottom-up network approaches may enable the design of sustainable and resilient agroecosystems (Ramankutty et al., 2018).

In particular, in- and off-crop management strategies have been proposed as methods for harnessing provisioning agricultural ecosystem services (Pretty et al., 2018). Field margin management is a prime example of off-crop management that is widely used in agri-environment schemes to boost ecosystem service provision, for example, pest control (Skellern & Cook, 2018) and pollination (Haddaway et al., 2018). The premise of these methods is that plant species can, via their demographic effects on other taxonomic groups at the community level, maximise biodiversity and generate ecosystem services (Scherber et al., 2010). As an example, studies on flower strips across North America, Europe and New Zealand have generally shown positive, albeit highly variable, effects on pollination (Albrecht et al., 2020). Multiple ecological processes, however, are rarely assessed in such examples, potentially omitting important trade-offs and synergies in the provision of ecosystem services (pollination, pest control and nutrient cycling) and disservices (herbivory) across agroecosystems.

Assessing the relative importance of plant species is a first step in determining the most effective in- and off-crop management strategies. Existing methods have focused on statistical and theoretical models (Montoya et al., 2019, 2020), with few field-based studies investigating the trade-offs between ecosystem services and disservices associated with different plant management strategies (but see Dainese et al., 2016). It is important to empirically understand these trade-offs, as they have implications for designing sustainable management strategies. For example, agri-environment schemes designed to promote pollinators may not be effective in supporting multiple other ecosystem services (e.g. natural enemies of pests), and in worst case scenarios, management may generate unintended ecosystem disservices (e.g. greater abundances of crop pests). To this end, two main challenges must be addressed: (a) how findings from theoretical networks compare to those from natural environments; and (b) whether it is possible to develop management strategies that maximise ecosystem services, while minimising disservices.

Here we assess the importance of non-crop plant species in agroecosystems and evaluate potential trade-offs between plant-related ecosystem services and disservices. To do so, we develop multilayer network analyses that incorporate multiple species interaction types to identify plants contributing to multiple ecosystem services—providing an approach for informing off-crop management interventions (e.g. planting seed mixes in the margins of agricultural fields). We used the Norwood Farm dataset (Pocock et al., 2012a), one of the first examples of multilayer ecological networks and created in a real-world agricultural system, to explore two hypotheses: (a) some plant species are more important than others in supporting the species richness of pollinators, parasitoids of pests and herbivores; and (b) there will be trade-offs in the provision of ecosystem services associated with different mixes of plants, that is, managing plant species for individual ecosystem services (e.g. increase pollination or parasitism services) will not support the provision of other ecosystem services and may incur ecosystem disservices (e.g. herbivory). By doing so we aim to generate an approach suitable for land managers to select mixes of plant species to optimise the provision of ecosystem services and disservices.

2 | MATERIALS AND METHODS

2.1 | Multilayer ecological network

We used a subset of data from the Norwood Farm network (Pocock et al., 2012a). The field site was a 125-ha organic, mixed lowland farm in southwest England (Norwood Farm, Somerset, UK; 51°18.3′N, 2°19.5′W). The farm comprised 23 fields of arable (cereals) and grasses (short-term leys in rotation and permanent pasture). The multilayer network was constructed from six cultivated and six non-cultivated habitats (hereafter termed 'farmed' and 'non-farmed' respectively). Farmed habitats consisted of fallow (uncultivated arable fields), ley (rye grass and red clover; *Lolium* sp. and *Trifolium pratense*), new ley (rye grass and red clover sown in the previous year), permanent pasture, lucerne (*Medicago sativa*; grown for silage) and crops (spring-sown barley, oats, winter-sown oats, triticale and wheat; *Hordeum vulgare*, *Avena sativa*, ×*Triticosecale*, *Triticum* sp.). Unfarmed habitats included grass margins (5–10 m wide), mature hedgerow (height and width 4.1 ± 1.5 and 3.6 ± 1.4 m [*M* ± *SD*] respectively), new hedgerow (new planted, grass and young trees; height and width 1.8 ± 0.7 and 1.3 ± 0.3 m [*M* ± *SD*] respectively), rough ground (e.g. uncultivated areas around farm buildings and machinery storage areas), standing trees (mature isolated trees in fields) and woodland.

Habitats were subject to replicated monthly sampling over 2 years (2007–2008). Samples for each taxonomic group were collected from three to four randomly located transects per month. Interactions between different species were compiled from a range of methods including both observations and secondary literature. Interaction strengths for pairwise interactions were estimated from direct field measurements or abundance surveys in conjunction with methods detailed in Pocock et al. (2012a) and Pocock et al. (2012b). All data were up-scaled to provide a total per habitat (counts of organisms per transect area multiplied up to total habitat area) and then summed across all available habitat to provide a farm-scale abundance measure. The original networks consisted of plants and 11 groups of animals that interact with them: plant feeders (butterflies and other flower visitors, phytophagous insects, seed-feeding insects and granivorous birds and mammals) and their dependents (primary and secondary aphid parasitoids, leaf-miner parasitoids, seed-feeding insect parasitoids and rodent ectoparasites). More detail on the Norwood Farm network is available in previous publications (Evans et al., 2011, 2013; Pocock et al., 2012a).

In this study, we used a subset of the Norwood Farm network to create a multilayer network comprised of three animal groups interacting with shared plants (flower visitors, phytophagous herbivores and leaf-miner parasitoids) exhibiting both mutualistic and antagonistic interactions. We selected these three groups of organisms as they are common across Norwood Farm and comprise three groups of ecological relevance to cropped habitats. This network included trophic, mutualistic and parasitic interactions among 381 animal and 78 plant taxa. This assumes interactions that convey ecosystem services (plant–pollinator and plant–herbivore–parasitoid), as well as disservices (plant–herbivore).

All analyses were conducted using R (R Core Team, 2021). Data and code are available at github.com/Royal-Society-Agricultural-Networks/multilayer-plant-importance.

2.2 | Selecting plant species mixes

Combining methods from network ecology and machine learning we aimed to predict which mixes of plant species balance the provision of ecosystem services (pollination and parasitism) and disservices (herbivory) at the farm scale.

We developed a genetic algorithm (GA) approach to identify plant species mixes that support optimal combinations of species richness across multiple groups of taxa (pollinators, parasitoids and herbivores). Here, species richness of these functionally important taxonomic groups is used as an indicator of ecosystem service and disservice provision (pollination, parasitism of pest insects and herbivory respectively). We used species richness in this study as it provides a measurable management target and abundance-based metrics are limited by the fact that it is difficult to untangle the effect of network structure on species abundances and vice versa (Guimarães, 2020; but see Fort et al., 2016). Similar methods, however, could be generalised to other aspects of community organisation and we present the results of our approach based on other metrics (abundance and evenness) in Appendix S1.

The basis for the GA approach is outlined in Figure 1 and is adapted from the study by M'Gonigle et al. (2017). Firstly, *N* initial networks, composed of *k* plant species and the taxa that interact with those plants, are randomly generated (Step A). The networks are then ranked based on f or f_m (Step B) which is an optimality metric (species richness) for the target taxonomic group or groups respectively. The highest ranked or 'best' mix is recorded, and the networks are then taken through 'selection' (Step C), 'recombination' (Step D) and 'mutation' (Step E). The next generation is then produced at the end of these steps (Step F). Steps B through F are then repeated either for a predetermined number of iterations (also termed generations) or until an optimal mix has been identified.

Using this general framework, it was possible to investigate bipartite and multilayer networks separately. For bipartite networks, f is simply the species richness of the individual taxonomic group interacting with the plant species in the mix (pollinators, parasitoids or herbivores). As an example, f for the plant–pollinator networks

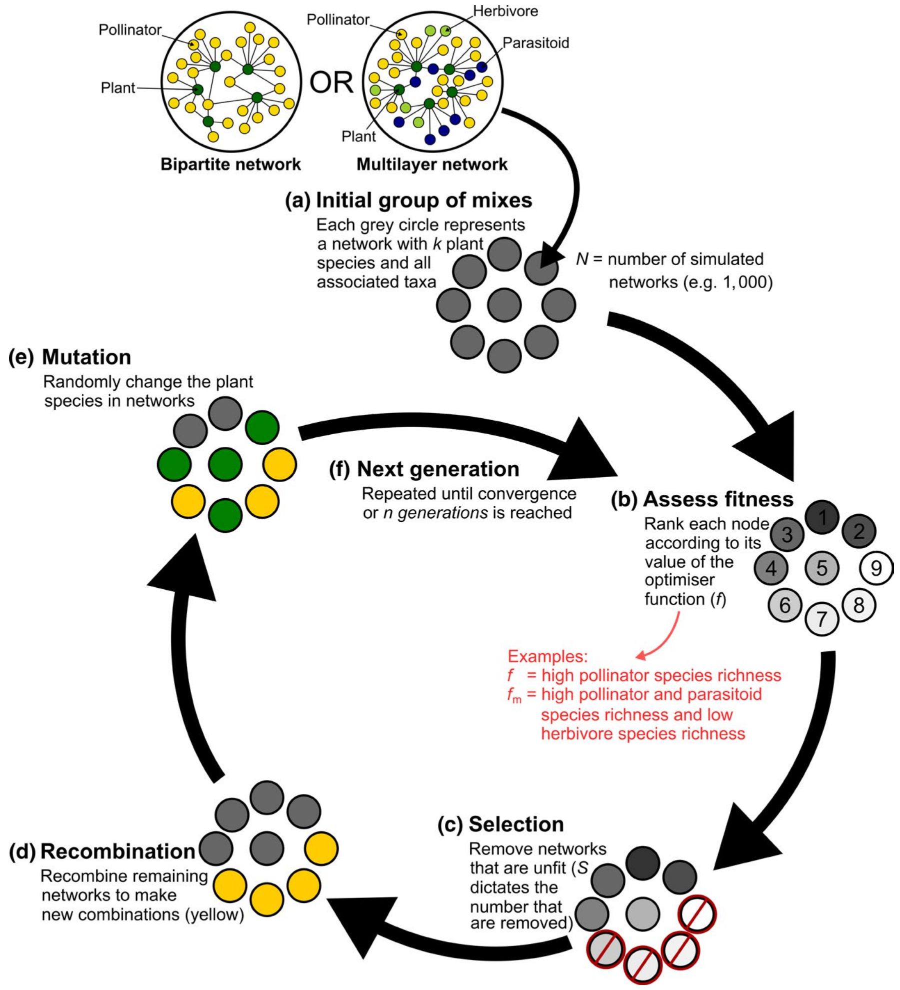

FIGURE 1 A conceptual representation of the genetic algorithm approach. (a) For either bipartite or multilayer networks, *N* initial groups of *k* plant species are randomly selected. (b) The plant mixes are ranked based on the optimiser function (which here is species richness but could be any property of the network of plants and interacting taxa). Individual (f) or compound (f_m) optimiser functions are used depending on the scenarios but see the red text for two examples. (c) The plant species mixes that have low values of the optimiser (i.e. low species richness) are removed from the pool of potential mixes. Plant species in the remaining mixes are recombined (d) into new mixes to replace the networks that are removed during the selection stage. In (e), random plant species not already in the mix are added to the plant mixes. Finally, the new plant mixes which have been altered from the initial mix defined in (a) are then taken through the entire process again (b–e). This continues until an optimal plant mix is identified, or until the maximum number of iterations is reached. All terms are referred to in the main text or code provided in Appendix S2

would be the maximum species richness of pollinators. For multilayer networks, the *f* for each bipartite network is combined into a compound function f_m, through the addition of the separate functions for each type of interactions (e.g. $f_m = f_1 + f_2 + f_3$, where f_n represents the optimising function for each bipartite network respectively). In this study, f_1 is maximum species richness of pollinators, f_2 is maximum species richness of parasitoids and f_3 is the minimum species richness of herbivores. Using this compound format means that it is possible to identify a mix of plant species that: (a) maximises the species richness of taxonomic groups associated with ecosystem services (pollinators and parasitoids); and (b) minimises the species richness of taxonomic groups associated with ecosystem disservices (herbivores).

2.2.1 | Management scenarios

Using the two types of GAs (bipartite and multilayer), we compared different types of management strategy. Firstly, those that focus on individual ecosystem services or disservices (e.g. selecting plant species that support the highest species richness of pollinators). Secondly, strategies that assess multiple taxonomic groups and integrate the trade-offs between services and disservices (i.e. selecting plant species that maximise both pollinator and parasitoid species richness, while minimising herbivore species richness). We produced algorithms to represent a range of management decisions (Table 1).

For each management scenario, we ran simulations for 1,000 generations. We also complete the process for different numbers of plant species in the mix ($k = 2$, 5 and 10) to understand the effect of the number of plant species on the results of the algorithms and the relative optimisation. We present the results from $k = 5$ in the main text, with results from other values provided in Appendix S1.

To verify the GA approach, we also compared the results of the GAs to other network indices commonly used to describe the importance of species: closeness centrality, betweenness centrality and normalised degree (Pocock et al., 2011), as well as the affinity of a plant species to important network modules. These data are available in Appendix S1.

2.3 | Sensitivity analysis for GAs

We completed a sensitivity analysis to understand the influence of different GA parameters, as well as producing uncertainty estimates. Analyses were performed using the Rocket High Performance Computing platform at Newcastle University.

We focused on the five dominant parameters (*N* the number of networks, *S* the selection strength, $P(m)$ the fraction of networks that mutate, $P(r)$ the fraction of the networks that recombine and $P(s)$ the fraction of the networks for 'sexual reproduction') from the GAs which could influence the plant mixes identified. Latin Hypercube Sampling (Stein, 1987), implemented using the 'lhs' package (Carnell, 2020), was used to randomly select a representative sample of values across the GA parameters. We generated 1,000 random combinations of the parameters. We then used these samples to parameterise the GAs and assess the optimal plant species mixes following the procedures outlined above (see Section 2.2).

We adopted a twofold approach to sensitivity analysis. First, we evaluated uncertainty in the identity of the plant species selected by determining the frequency with which plants are included in the optimal mixes. Here, low numbers of frequently identified species in the optimal mix would indicate low sensitivity to a given parameter. Second, we determined the variability in the species richness of each taxonomic group associated with the 1,000 plant mixes generated.

2.4 | Characteristics of multilayer networks associated with plant species mixes

Plant mixes derived for each management scenario (Table 1) were assessed in terms of their associated multilayer species interaction networks (plants, pollinators, parasitoids and herbivores). This provides information on how potential management interventions focusing on individual and multiple ecosystem services influence the structure of the multilayer network, and thus alter the provision of other ecosystem services. We calculated a range of different node and network properties.

2.4.1 | Degree distribution, connectance and Katz centrality

We calculated the mean degree, C_D ($\sum_{j=1}^{N} x_{ij}$), to provide an indication of the level of connectedness for each species. This metric included links spanning all included interactions. For example, if a species was both a pollinator and a parasitoid, the degree value would reflect mutualistic and antagonistic links. Second, we calculated connectance (I/s^2, where *I* are the links and *s* denotes the number of species) based on the same principle, treating both mutualistic and antagonistic links as equal in the multilayer network. Both metrics were calculated using the 'igraph' package (version 1.2.4.1; Csardi & Nepusz, 2006). Third, we calculated mean Katz centrality (Katz, 1953), using the 'centiserve' package (Jalili et al., 2015). Katz centrality describes how central a species is by considering the direct and indirect pathways connecting a species in the network (Guimarães et al., 2017). For each node, centrality was calculated following $x_i = \alpha \sum_j A_{ij} x_j + \beta$.

2.4.2 | Weighted robustness

Robustness, the tolerance of networks to coextinctions resulting from primary extinctions (Albert et al., 2000), provides a valuable insight into the structure of a network and its likely resilience to

TABLE 1 Management scenarios, expected outcomes, required information and genetic algorithm (GA) approach implemented

Management strategy (*intervention*)	Expected outcomes	Information required from GA for management	GA type (*name*)
Maximise pollination (*planting beneficial plants species*)	Pollination ↑ Parasitism ? Herbivory ?	Plants supporting high pollinator species richness	Bipartite (*Pollinator*)
Maximise parasitism of insect pests (*planting beneficial plant species*)	Pollination ? Parasitism ↑ Herbivory ?	Plants supporting high parasitoid species richness	Bipartite (*Parasitoid*)
Minimise herbivory of crops (*removing nuisance plant species*)	Pollination ? Parasitism ? Herbivory ↑	Plants supporting high herbivore species richness	Bipartite (*Herbivore*)
Maximise ecosystem services and minimise disservices (*planting beneficial plants*)	Pollination ↑ Parasitism ↑ Herbivory ↓	Plants supporting high pollinator and parasitoid species richness and low herbivore species richness	Multilayer (*Multilayer*)

TABLE 2 Plant species mixes identified using bipartite and multilayer genetic algorithms. Data for all combinations of *f* and *k* are presented in Appendix S1

Plant species mix	Plant species
Pollinator	Hogweed (*Heracleum sphondylium*) Cow parsley (*Anthriscus sylvestris*) Creeping thistle (*Cirsium arvense*) Creeping buttercup (*Ranunculus repens*) Mayweed sp. (*Matricaria* sp.)
Herbivore	Creeping thistle (*Cirsium arvense*) Grass spp. (Poaceae spp.) Stinging nettle (*Urtica dioica*) Sow thistle (*Sonchus* sp.) Clover sp. (*Trifolium* sp.)
Parasitoid	Creeping thistle (*Cirsium arvense*) Creeping buttercup (*Ranunculus repens*) Grass spp. (Poaceae spp.) Blackthorn (*Prunus spinosa*) Oak sp. (*Quercus* sp.)
Multilayer	Hogweed (*Heracleum sphondylium*) Creeping thistle (*Cirsium arvense*) Creeping buttercup (*Ranunculus repens*) Mayweed sp. (*Matricaria* sp.) Grass spp. (Poaceae spp.)

future changes (Bascompte & Stouffer, 2009). Individual bipartite networks, as well as the total multilayer network, were analysed using an amended version of the deterministic avalanche model (DA) as described in the study by Bane et al. (2018). Briefly, a randomly selected primary (plant) extinction may produce secondary (pollinators, herbivores) and tertiary (parasitoids) extinctions that leave plants with less than a fraction T (here set at 0.5) of their observed interactions with pollinators. If this occurs, there is a ‘coextinction avalanche’ due to plant extinctions from the loss of pollinators, which follows a non-random pattern determined by the structure of the network. These cascades continue until there are no further secondary extinctions. Then a new, random primary extinction candidate or ‘trigger’ is specified, and the process starts again. We then calculate the robustness (R) of the overall multilayer network following

$$R = \frac{1}{AP}\sum_{p=0}^{P} a(p),$$

where p is the number of plant species that have gone extinct (from 0 to P), $a(p)$ is the number of pollinator species remaining in the network (from A to 0) and R is the normalised ($0 < R < 1$) area under the curve of a graph (the proportion of plant nodes that have gone extinct against the proportion of surviving pollinator nodes; Burgos et al., 2007). Values close to 1 indicate high robustness of networks to primary extinctions. As R is dependent upon the order of extinctions, we run 1,000 random extinction sequences to produce a representative frequency distribution, $f(R)$.

2.4.3 | Stability

Plant species mixes and their associated pollinator, herbivore and herbivore–parasitoid networks were assessed in terms of ecological stability. In this study, stability refers to the resilience of the plant mix and its associated network. Thus, we adopt engineering resilience, the ability of a system to return to a stable state after a disturbance, when assessing stability (Holling, 1996).

Stability was calculated following the study by Sauve et al. (2015). Briefly, for each network, a community matrix (J), which is the Jacobian matrix from a population dynamic model at equilibrium with all species present ($\{I, j\} \in 1, S_{\text{plant}} + S_{\text{animal}}$), was estimated. The elements of the matrix (J_{ij}) quantify the effects of species j on the growth rate of species i. For mutualistic interactions, the effects of species i on species j, and vice versa, are positive. For antagonistic interactions, where species i is the consumer, the effect of interactions is positive for species i but negative for species j. From the Jacobian matrices, stability was calculated as the minimum intraspecific competition, or self-damping, required for community stability (cf. Neutel et al., 2002, 2007). This appears as $J_{ii} = -s$, with a minimum value of s such that all eigenvalues have negative real parts (Sauve et al., 2015).

3 | RESULTS

3.1 | Plant species mixes identified using bipartite methods

Mixes of plant species generated by bipartite GAs highlighted a number of different plant species responsible for maximising the species richness of pollinator, parasitoid and herbivore taxa (Table 2). There was substantial overlap in the plant species selected across the plant mixes. Two plant species, creeping buttercup *Ranunculus repens* and creeping thistle *Cirsium arvense*, were identified as maximising the species richness of both pollinator and parasitoid taxa (Table 2). Creeping thistle, however, was also associated with high species richness of herbivores. A range of other plant species were more variably associated with high levels of pollinator, parasitoid and herbivore species richness in the ecological network and were not observed in multiple plant mixes (Table S1).

3.2 | Plant species mixes identified using the multilayer approach

The multilayer GA produced a mix of plant species that maximised the richness of pollinator and parasitoid species, while minimising the species richness of herbivores (Table 2). Similarities were observed between this plant mix and the mixes selected using bipartite GAs. Specifically, Hogweed *Heracleum sphondylium*, Creeping thistle *Cirsium arvense* and Mayweed *Matricaria* sp. were identified as generating high pollinator species richness, but also high herbivore species richness in the case of Creeping thistle *Cirsium arvense*. In these cases, in the multilayer GA framework, the positive effect of the plant species on parasitoid and pollinator species richness, respectively, overrode the negative effects presented by their positive role in increasing herbivore species richness.

Each of the plant species mixes supported different levels of species richness(s) across the three taxonomic groups (Figure 2). The multilayer GA plant species mix performed the best in terms of jointly maximising the species richness of pollinators ($s = 174$) and parasitoids ($s = 63$), while minimising the species richness of herbivores ($s = 9$). Species richness of parasitoids in the multilayer plant species mix was not as high as that from the bipartite GA plant mix focusing on maximising parasitoid species richness ($s = 74$). Yet the species richness (s) of herbivore generated by the multilayer GA plant mix was marginally lower ($s = 9$) compared to the other plant species mixes ($\overset{!!}{s} = 9.5 \pm 0.9$ *SE*). The bipartite GA maximising pollinator species richness was the best performing bipartite method, supporting high pollinator species richness ($s = 169$) and low herbivore species richness ($s = 8$); however, it supported low species richness of parasitoids ($s = 44$).

3.3 | Sensitivity analysis for GAs

Plant mixes from GAs had relatively low uncertainty, with no significant relationships between parameters and either species richness of selected plant mixes or the variation in species richness (Figures 2 and 3). Multilayer GAs were more sensitive than bipartite GAs to changes in algorithm parameters (Figure S1). This translated to greater levels of variation in both mix composition and species richness of associated taxonomic groups (Figure 2). The higher levels of variation in the results of the multilayer GA result from the compound optimising function (f_m), which aggregates the uncertainty and variability present in each layer of the ecological network.

Despite variation in species richness, the identities of the plants present in the optimal mixes were relatively consistent, with only a small suite of species present in the optimal plant mixes. As with the variability in the species richness across mixes (Figure 2), however, the multilayer GA exhibited higher variation in species identities. Across the 1,000 iterations of the multilayer GA, a greater number of plant species present in at least one of the optimal mixes ($n = 68$) in comparison to the mean value for the bipartite subnetwork GAs ($\overset{!!}{n} = 26.7 \pm 5.2$ *SE*). As a result, each of the species was also present in a lower proportion of the optimal mixes (Figure 3).

3.4 | Assessing networks associated with plant species mixes

The ecological networks associated with the plant species mixes selected by GAs exhibited a range of properties (Table 3). Generally, networks associated with the multilayer GA plant mix provided a well-connected and stable network of plants, pollinators, herbivores and parasitoids (Table 3; Figure 4). The multilayer plant mix network combines plants that are strongly associated with high species richness of a single taxonomic group (Figure 4). In comparison, the pollinator plant species mix selected plants that individually supported a high species richness of pollinators and also supported parasitoid and herbivore species richness.

4 | DISCUSSION

Managing agroecosystems to provide multiple ecosystem services is extremely challenging, but it is the overarching aim of many agricultural schemes. Here, using a network approach, we show that a series of trade-offs may exist when managing plant species to maximise ecosystem services and minimise ecosystem disservices in agricultural environments. Specifically, managing plant species to promote individual ecological processes (e.g. pollination) may lead to the unintended maximisation or minimisation of other functions, such as parasitism or herbivory. Through providing a computational framework for assessing the optimal plant species mixes for multiple ecosystem functions, we also highlight that simple solutions have the potential to provide effective management options. We showed the effectiveness and utility of these novel methods using an example dataset from organic farmland. In the case of a multilayer network from Norwood Farm (plants, pollinators, herbivores and parasitoids), selecting a mix of plant species that maximised the species richness

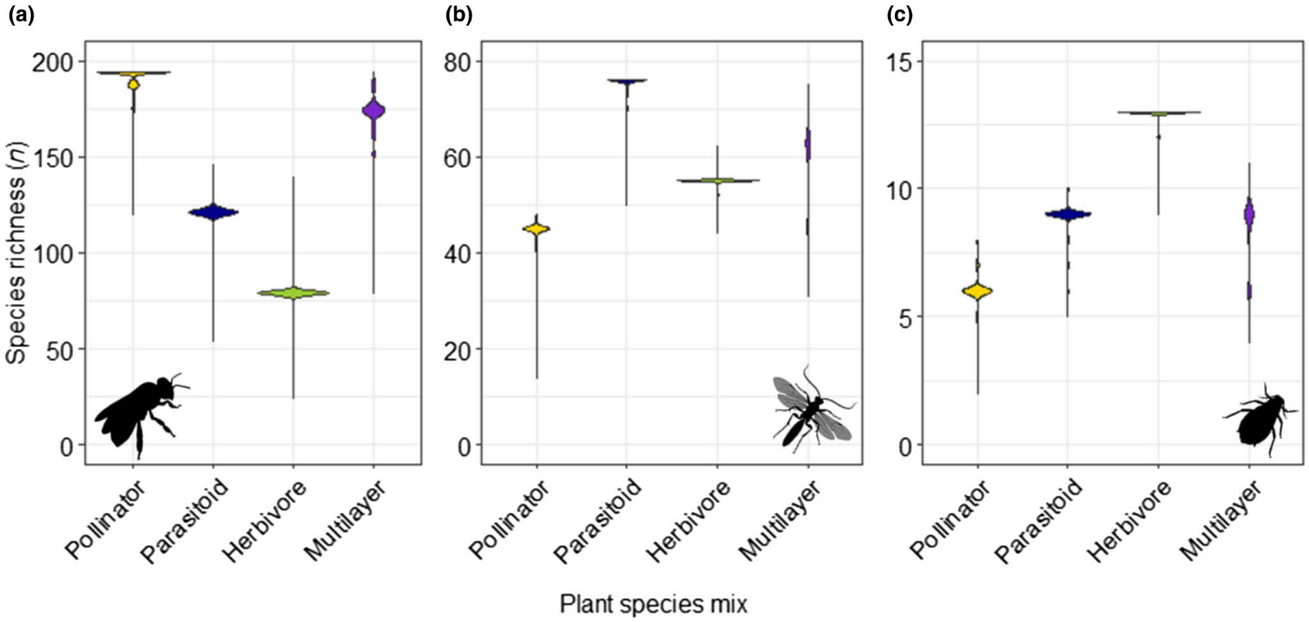

FIGURE 2 Differences in species richness of (a) pollinators, (b) parasitoids and (c) herbivores between plant mixes from bipartite and multilayer genetic algorithms. Data in the violin plots are generated from 1,000 random simulations as described in Section 3.3. Images are from Phylopic.org CC-BY 2.0

of pollinators also supported a high species richness of leaf-miner parasitoids (i.e. parasitism of pest insects), while supporting a relatively low species richness of herbivores. The more complex method trialled here (multilayer GA), more effectively minimised the species richness of herbivores, while not compromising the stability, robustness and connectance of the associated ecological networks. Acknowledging the limitations (see below), this provides a valuable new framework for arable land managers and policymakers, and as such we provide a user-friendly protocol for the implementation of the methods described in Appendix S3.

Trade-offs in ecosystem processes and services were apparent across an agricultural network. Similar trade-offs resulting from agricultural management have been previously shown by theoretical models (Montoya et al., 2019), economic evaluations (Kragt & Robertson, 2014) and literature reviews (Power, 2010). Nevertheless, here we show direct empirical evidence demonstrating the potential trade-offs in ecosystem processes and services resulting from management decisions in agroecosystems. When managing agroecosystems, it is therefore important to recognise that interventions may not have the desired or expected effects as a result of the trade-offs, synergies and other interactive effects present within ecological networks and their subsequent effects on ecosystem functioning. Moreover, merging species interaction networks (e.g. trophic and non-trophic) is crucial for understanding the potential effects of management on the structure and function of agroecosystems.

Here we provide a multilayer method for managing trade-offs in ecosystem functions and services/disservices. The approach provides a straightforward and intuitive way to select plant mixes which could be sewn or selectively maintained within the margins of arable fields. There are, nevertheless, a number of caveats of this study. Firstly, species interaction data and subsequent analyses were conducted at the farm scale (125 ha) which incorporates multiple habitats (see Pocock et al., 2012a). As a result, it is assumed that organisms interacting with the non-crop plants across all habitats are able to spillover into crop habitats. For the analysis of the Norwood Farm network, this assumption holds as there is a large mixture of different non-crop and crop habitats, most of which are juxtaposed with each other. Furthermore, many species within the network are generalists, observed across multiple habitats and interacting with a large number of other organisms. In the future studies, across more spatially isolated habitats, there would need to be care taken to identify those plant species that are in close enough proximity to provide spillover effects to proximal crops. Secondly, Norwood Farm is an organic farm with a mixture of cropped and non-cropped habitats. Thus, the abundance, diversity and importance of weed species and other non-crop plants within ecological networks may be enhanced as a result of the management techniques (Norton et al., 2009). Similar analyses carried out across non-organic farms may not support the findings above illustrating the importance of non-crop, weed plant species. It is therefore important to collect species interaction data across other agricultural habitats, especially when looking to assess the effectiveness of management interventions (Gray et al., 2014). This can be achieved through a variety of methods from novel metabarcoding (Evans et al., 2016), inferring networks from existing datasets (e.g. Biological Records Centre Database of Insects and their Food plants https://www.brc.ac.uk/dbif/ and iSpot https://www.ispotnature.org/) or directly observing interactions in the field. Thirdly, and perhaps most importantly, this study infers ecosystem service provision from species richness of organisms involved in key ecosystem processes (e.g. pollination). This is a valid assumption

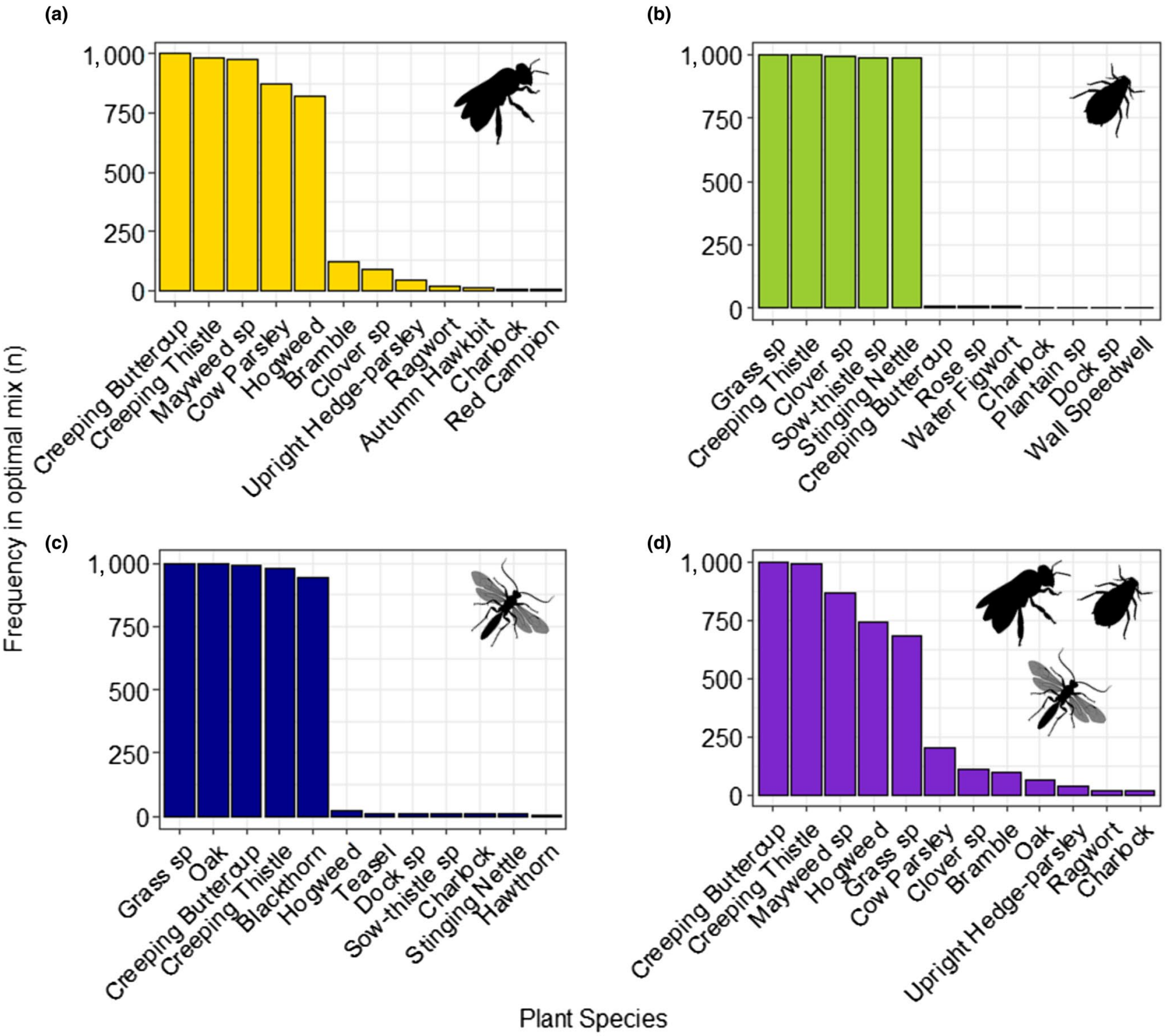

FIGURE 3 Plant species frequency in optimal mixes during sensitivity analyses ($n = 1{,}000$). The top 10 most frequently selected plant species for bipartite subnetwork genetic algorithms (GAs) (a) pollinator, (b) herbivore and (c) parasitoid as well as (d) the multilayer GA

TABLE 3 Properties of the species interaction networks associated with the single most optimal plant mixes from bipartite and multilayer genetic algorithms

				Species richness (s)			Robustness (R_Q)			
Plant mix	Mean degree (d)	Mean Katz centrality	Connectance (l/s^2)	Poll	Para	Herb	Poll	Para	Herb	Stability (S_b)
Pollinator	2.75	1.65	0.011	194	45	6	0.50	0.38	0.29	12.05
Parasitoid	2.53	1.58	0.012	121	76	9	0.32	0.53	0.32	11.57
Herbivore	2.61	1.42	0.017	79	55	13	0.27	0.44	0.38	9.90
Multilayer	2.76	1.65	0.011	174	63	9	0.41	0.52	0.36	12.13

as in many cases diversity within functional groups, for example, plants, conveys a greater level of ecosystem functioning (see Isbell et al., 2017). Nevertheless, it is also apparent that the relationships between biodiversity and ecosystem functioning/services are highly variable (van der Plas, 2019). The method also does not account for a range of other important factors, such as trait distributions in

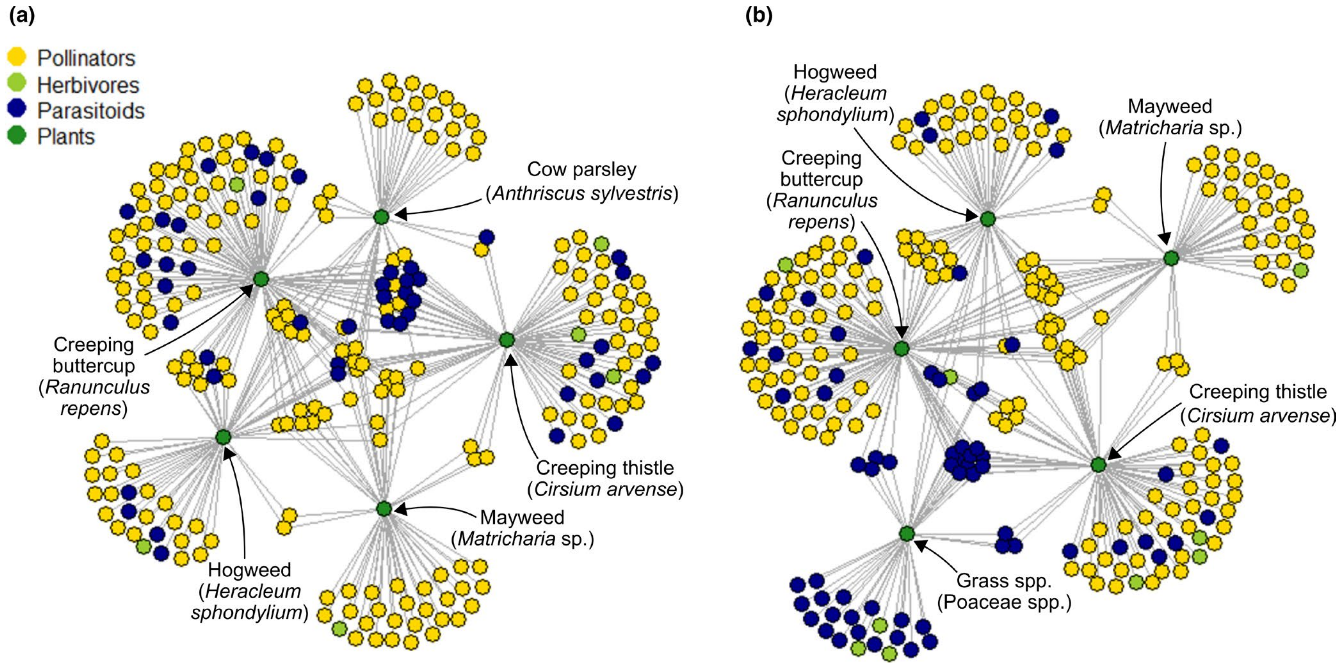

FIGURE 4 Examples of ecological networks associated with plant mixes. (a) Maximising pollinator species richness (bipartite network) and (b) maximising both pollinator and parasitoid species richness and minimising the species richness of herbivores (multilayer network)

plant mixes (e.g. flowering phenology, flower morphology and nectar provision), which may influence the importance of plants and the extent to which they contribute to ecosystem services within the environment (Dormann et al., 2017). Future studies should thus look to combine network analyses with trait analyses and measures of ecosystem function or service provision to better understand the direct links between important species and trade-offs in ecosystem service provision in agroecosystems (Manning et al., 2019). Research around pests and beneficials provides a suitable starting point in agroecosystems as species interaction research surrounding these groups has long taken place in these environments.

Based on our findings, we recommend that landowners consider the use of high levels of biodiversity and off-crop management in the farms to ensure the delivery of provisioning ecosystem services (pollination and pest parasitism) and, consequently, reduce the costs inverted in pest control and herbivory of the crops. The next stage for this field of research is to test the accuracy of these predictions in other field scenarios by experimentation. Future studies should look to combine an initial assessment of plant importance within agricultural networks aimed at identifying non-crop plant species that should be promoted, with a secondary manipulation of plant abundance either by planting or selective removal of non-target species. Such assessments would contribute further towards the development of a predictive form of network ecology that can be used to inform decision-making and develop agroecosystems that support biodiversity as well as sustainable and productive food systems. In agricultural systems, this is a real possibility as network structure and complexity can be linked to plant reproductive success (seed set and quality)—data which are routinely collected for crops. We highlight how this can be implemented in different study systems in Appendix S3.

5 | CONCLUSIONS

Predictive network ecology appears an effective tool for identifying mixes of non-crop plant species that balance the trade-offs between ecosystem services (pollination and parasitism of pest insects) and disservices (herbivory) in agroecosystems. Here we develop a method able to select mixes of plant species that both maximise the species richness of pollinators and parasitoids, while minimising the species richness of herbivores. We show that ecological network approaches can be utilised at the heart of farm management and are ready to be developed and implemented in practice. More broadly, our study raises some interesting questions surrounding potential trade-offs associated with manipulating biodiversity in agroecosystems to improve the provision of vital ecosystem services.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

F.M.W. and D.M.E. conceived the ideas and designed the methodology; F.M.W. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are previously published and available via the Dryad Digital Repository https://doi.org/10.5061/dryad.3s36r118 (Pocock et al., 2012b).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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