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Differential effects of fertilisers on pollination and parasitoid interaction networks

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Abstract

1. Grassland fertilisation drives non-random plant loss resulting in areas dominated by perennial grass species. How these changes cascade through linked trophic levels, however, is not well understood.
2. We studied how grassland fertilisation propagates change through the plant assemblage into the plant–flower-visitor, plant–leaf miner and leaf miner–parasitoid networks using a year's data collection from a long-term grassland fertiliser application experiment. Our experiment had three fertiliser treatments each applied to replicate plots 15 m^2 in size: mineral fertiliser, farmyard manure, and mineral fertiliser and farmyard manure combined, along with a control of no fertiliser.
3. The combined treatment had the most significant impact, and both plant species richness and floral abundance decreased with the addition of fertiliser. While insect species richness was unaffected by fertiliser treatment, fertilised plots had a significantly higher abundance of leaf miners and parasitoids and a significantly lower abundance of bumblebees. The plant–flower-visitor and plant–herbivore networks showed higher values of vulnerability and lower modularity with fertiliser addition, while leaf miner–parasitoid networks showed a rise in generality.
4. The different groups of insects were impacted by fertilisers to varying degrees: while the effect on abundance was the highest for leaf miners, the vulnerability and modularity of flower-visitor networks was the most affected. The impact on the abundance of leaf miners was positive and three times higher than the impact on parasitoids, and the impact on bumblebee abundance was negative and double the magnitude of impact on flower abundance.
5. Overall, our results show that while insect species richness was unaffected by fertilisers, network structure changed significantly as the replacement of forbs by grasses resulted in changes in relative abundance across trophic levels, with the direction of change depending on the type of network.
6. *Synthesis*. By studying multiple networks simultaneously, we were able to rank the relative impact of habitat change on the different groups of species within the community. This provided a more holistic picture of the impact of agricultural

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intensification and provides useful information when deciding on priorities for mitigation.

KEYWORDS
ecological networks, fertiliser, flower–pollinator network, grasslands, insect, parasitoid, parasitoid web, pollinator

1 | INTRODUCTION

Nutrient enrichment is one of the most common causes of plant species decline worldwide (Hautier et al., 2015; Tilman et al., 2001). In grasslands, nutrient enrichment leads to the dominance of plant taxa, such as perennial grasses. Plant species that can capitalise on increased macronutrient supply increase their biomass production, filling gaps and growing taller, thereby intercepting light at the expense of shorter or less competitive species (Harpole et al., 2016). The net result is a reduction in diversity as forb species are replaced by grass species (Phoenix et al., 2012). In the United Kingdom, and in the rest of Europe, the most common source of nutrient enrichment in grasslands is fertilisation which has led to the transformation of extensive areas of diverse grasslands into intensively managed low diversity grasslands (Ridding et al., 2015). While fertiliser application rates have dropped in the United Kingdom in the last decade (DEFRA, 2019), global usage and the associated negative effects are expected to increase (FAO, 2017).

The effects of grassland fertilisation on plant diversity are well documented (see Harpole et al., 2016; Phoenix et al., 2012), and while its effects on insects communities are well described (e.g. Andrey et al., 2014; Fountain et al., 2008; Haddad et al., 2000), the impact of fertilisers on the ecological network of species interactions is still not well understood as just a handful of studies have used a network approach. The network of interactions among species affects how resilient the community is to perturbation (Ings et al., 2009), how it responds to the arrival of novel pests (Macfadyen et al., 2009), how robust it is to species loss (Solé & Montoya, 2001) and how it could be affected by climate change (e.g. Burkle et al., 2013). Moreover, in managed habitats such as agricultural land or forestry, these interactions provide ecosystem services such as pollination and pest control. In short, understanding how the addition of fertilisers affects the interactions among species is important if we are to understand its impact and be able to mitigate its effects.

So far, the studies which consider the impact of fertiliser addition using a network of species interactions approach do not consider the cumulative effects of the nutrient inputs that occur in the productive systems where fertilisation occurs every year. This is because they are short-term experiments studying a single nutrient (e.g. Burkle & Irwin, 2009), are run in monocultures which miss the effects triggered by changes in the plant community (e.g. Lohaus et al., 2013); or they analyse spatial gradients rather than experimental manipulations (e.g. Fonseca et al., 2005). Moreover, no researchers have considered more than a single type of network simultaneously, making it difficult to determine the overall response of insect communities to the addition of fertilisers and impossible to rank its effects on the different components of communities. Previous studies have however provided useful information on the impact of fertilisers on insect communities. For example, nutrient addition can lead to decreased insect herbivore and pollinator species richness by reducing host plants and floral resources (Potts et al., 2010), but it can also lead to increased abundance (Pöyry et al., 2017) and biomass (de Sassi & Tylianakis, 2012) of herbivore species that feed on nitrophilous plants (Smart et al., 2000). Parasitoids may respond to increased biomass in the herbivore community by choosing bigger species, thus decoupling species-level responses (de Sassi, Staniczenko, et al., 2012; de Sassi & Tylianakis, 2012; Stiling & Moon, 2005). These effects, particularly the loss of species richness, may reduce the stability of the ecological network, making the system more sensitive to species extinction (Solé & Montoya, 2001).

We address the lack of evaluation of the cumulative effects of fertilisers and expand upon the single network focus of previous work by using a 26-year-old well-replicated experimental grassland manipulation. Thus, our data which are collected from a single field season use an approach which combines long-term effects on the plant community with high statistical power. We add a new dimension by considering three types of ecological network simultaneously: plant–leaf miner networks, leaf miner–parasitoid networks and plant–flower-visitor networks. This allows us to rank the impact of fertiliser loads on these three different components of the community. Using this long-term experimental system and studying three different insect networks simultaneously, we asked four questions: Q1: Does grassland fertilisation affect the species richness and abundance of plants, flower visitors, leaf miners and parasitoids? Q2: Does grassland fertilisation alter the network of species interactions, that is, the structure of the interactions among species? Q3: What is the relative magnitude of change in the four components of the system; plants, flower visitors, leaf miners and parasitoids, in response to fertilisation? Q4: Are any changes in the network which are attributable to grassland fertilisation, mediated by changes in plant species dominance?

2 | MATERIALS AND METHODS

2.1 | The field experiment: Colt Park Meadows

Colt Park Meadows is a long-term nutrient manipulation experiment located at 300 m elevation in the Ingleborough National Nature Reserve in the Yorkshire Dales, northern England (54°12′N, 2°21′W). The experiment started in 1990 on permanent grassland dominated by

the perennial grass species *Lolium perenne* and *Cynosurus cristatus*, on a shallow brown-earth soil (pH 5.1) over limestone of moderate–high residual fertility (15 mg P2O51-1). The original aim of the experiment was to test different management strategies for improving the plant species diversity of grasslands on a working farm (Smith et al., 2008). Thus, the data are collected in the context of a working agricultural pastoral, grassland system, providing an opportunity to explore the effect of fertiliser on the dominant agricultural land use in the United Kingdom (Nafilyan & Office for National Statistics, 2015).

The experiment consisted of 72 plots, each 2.5 m × 6 m (15 m^2) in size, arranged in three blocks of 24 plots. In each block, six plots were randomly assigned to each of three fertiliser treatments: (a) mineral fertiliser application (in the ratio 20 N:10 P:10 K, hereafter NPK; 25 kg/ha nitrogen plus 12.5 kg/ha of P2O2 and K2O), (b) farmyard manure (12 t/ha, hereafter FYM), (c) both fertilisers together (hereafter NPK + FYM), along with a control of no fertiliser. While there are control plots for fertiliser application, there are no grazing controls as grazing is ubiquitous in these upland pastoral systems. To control for grazing is nonsensical as the experiment was set up to restore grasslands in grazed systems by improving management practices, this including fertiliser addition (e.g. Cole et al., 2019; Smith et al., 2003, 2008).

In UK grassland, FYM is commonly applied as part of the traditional management regime for growing seasonal grass forage. NPK, as mineral fertiliser, is used in intensive conventional farming to increase forage production. Per fertiliser treatment, there were 18 plots (Figure S1). All treatment and control plots were subject to the same seasonal grazing and forage harvesting regime as follows: sheep grazing from March to mid-May, application of the fertiliser treatments in late May, hay cutting after 21 July, then sheep grazing for 2 weeks, followed by cattle grazing during early winter. Our sampling took place in 2016, after stock removal and before cutting.

2.2 | Sampling plants, flowers and insects

To assess changes in plant species composition, we used data on plant species richness and % cover from 2014, which was the most recent full vegetation survey. In the vegetation survey, species were recorded within a 2 × 2 m quadrat divided and pin-hits of each species counted at each 20 × 20 cm intersection. Percentage cover was calculated by counting the number hits of each species out of the total (see Suplementary Information, Plant survey). Plant surveys were run every 2 years throughout the experiment until 2014; analysis of species changes shows a consistent trend in the effect of fertilisers treatments for the last decade (Allinson & Natural England, 2014). To directly compare floral resources and flower visitors in 2016, we sampled flower abundance in each of the 72 plots during late May to early June and again 3 weeks later. For each sample, we placed three transects of 30 cm × 5 m lengthwise regularly in each plot, we counted all flowers within the transect and identified them to species. In each of the two sampling rounds, transects were positioned in a different location to sample the whole plot area. On the same transects, leaf miners were collected (for a total of *c*. 190 hr) and reared individually until an adult leaf miner or a parasitoid emerged. Within 24 hr of each flower abundance survey, we spent 8 min in each plot between 09:00 and 17:00 hr surveying flower-visiting insects for a total of 19.2 hr of sampling. Insects were collected using a hand net. Bumblebees (*Bombus* spp.) were caught, identified in the field and released. Other flower-visiting insects and adult leaf miners were identified by professional taxonomists (see Acknowledgements). Parasitoids were sent to the Canadian Centre for DNA Barcoding (Guelph Canada) for identification. To assign an identification, we used methods available from within the Barcode of Life Data Systems (BOLD) refined by inspection of indentation trees. BOLD automatically assigns all DNA sequences length index numbers (BINs). Based on the BOLD indentation tree, we examined the BINs associated to our sequences and give a name after comparing representative BINs to the BOLD reference collection (Hebert et al., 2003; Ratnasingham & Hebert, 2007; see Supporting Information, Molecular Analysis). Assigned names were then reviewed by an expert in parasitoid taxonomy (see Acknowledgements) to confirm placements.

2.3 | Data analysis

We estimated sampling completeness using the abundance-based richness estimators Chao1 in the VEGAN R package (Oksanen et al., 2019; R Core Team, 2019). Percentage sampling completeness was calculated by dividing the observed richness by the estimated total richness and multiplying by 100 (Chacoff et al., 2012).

Q1: Does grassland fertilisation affect the species richness and abundance of plants, flower visitors, leaf miners and parasitoids?

We used linear mixed-effect models to test for treatment effects on flower, flower visitor, herbivore and parasitoid abundance and species richness. We considered levels of fertiliser as fixed effects. Block was treated as a random effect to address the non-independence between plots within the same block. We assessed the normality of residuals using the Shapiro test, and the variance homogeneity of the residuals visually. Abundance and species richness were log(x + 1) transformed, except for parasitoid abundance which we analysed using a negative binomial distribution. Given the interest in bumblebees as pollinators, we considered these separately as well as collectively with other pollinators, but as species richness was low (mean per plot = 1), we only analysed their abundance. Also, after testing for overdispersion we used a quasi-Poisson distribution for comparisons of bumblebee abundances (Table S4). We discarded zero-inflation in the bumblebee data after testing observed versus expected numbers of zeroes using a modified version of the checking function in Lunn et al. (2013; Supporting Information for R code). Models were run with and without up to one outlier. We report the values of the model without the outlier when it provided a better fit. Models were fitted using the R packages LME4 (Bates et al., 2015) and GLMMTMB (Brooks et al., 2017).

We conducted Post-hoc analyses using Tukey tests in the package MULTICOMP (Hothorn et al., 2008; R Core Team, 2019).

Q2: Does grassland fertilisation alter the network of species interactions?

For each of the three component networks, plant–flower visitor, plant–leaf miner and leaf miner–parasitoid, we calculated three quantitative network metrics: vulnerability, generality and modularity. Vulnerability is the mean number of species of the higher trophic level per species of the lower trophic level (i.e. number of insect species per plant species). Generality is the mean number of species of the lower trophic level per species of the higher trophic level (here, the number of plant species per insect species, or number of insects per parasitoid species). Together, these two metrics capture changes in the distribution of links between trophic levels in the networks. Increased vulnerability indicates increasing dependency of the insect community on fewer plant species or for the parasitoids on fewer host species. In contrast, increased generality indicates an expansion of the range of species attacked, an increase in the abundance of generalist species or both. The two metrics were weighted by their marginal totals (Bersier et al., 2002). Modularity is found in both mutualistic and antagonist networks (Dormann et al., 2017) and it can affect the resilience of networks to extinction events (Stouffer & Bascompte, 2011). Technically, modularity evaluates the degree in which the network is partitioned into interconnected subsets of interacting species. We calculated weighted quantitative modularity using the DIRTLPA + algorithm (Beckett, 2016). Modularity ranges from 0 (which means the network does not have more links within modules than expected by chance) to 1 (when all links are within modules). A high value of modularity indicates both a high stability and specialisation (Dormann et al., 2017).

We calculated the three network metrics using the R package BIPARTITE (Dormann & Gruber, 2011; R Core Team, 2019). We used linear mixed-effect models to test for treatment effects on network structure metrics, following the methods used for Q1. Where necessary, metrics were transformed to meet the assumptions of normality (Table S5). For modularity, we accounted for the effect of network size by including species richness as a co-variable in the model.

Q3: What is the relative magnitude of change in the four components of the system, plants, flower visitors, leaf miners and parasitoids, in response to fertilisation?

We focussed on the comparison of control and treatment-related changes in species richness, abundance, vulnerability and generality. We compared the relative magnitudes of the strongest fertiliser treatment (FYM + NPK) on each metric by comparing their standardised effect sizes, which are equivalent to the standardised regression parameters from each model. Thus, each coefficient estimates the biological response to fertiliser compared to the control, in units of standard deviation. All four metrics were calculated for flower visitors, leaf miners and parasitoids; for forbs and flowers, species richness and abundance were calculated, respectively.

Q4: Are any changes in the network which are attributable to grassland fertilisation, mediated by changes in plant species dominance?

We used structural equation modelling (SEM; PIECEWISESEM R package; Grace et al., 2010; Lefcheck, 2016) to test whether the effect of the fertiliser treatments on the networks was mediated from plants to insects via non-random changes in the plant community (Figure 1). Using data on plant percentage cover and biomass from previous research at Colt Park Meadows (Allinson & Natural England, 2014; Ward et al., 2016; see Figures S2–S4), we identified plant species that had persisted or increased in response to the treatments. Differences in % of cover and biomass of identified groups of plants between the treatments were tested with a linear mixed model following methods used for Q1. We hypothesised that these 'winning' plant species would exert strong control on the abundance and distribution of insect species and their interactions in the dependent networks. Their importance in the structure of the network was measured by the degree metric (the number of interactions the plant species has with insect species; see Pocock et al., 2011). To test for mediation, we evaluated change in the significance level and AIC values of SEM models with and without

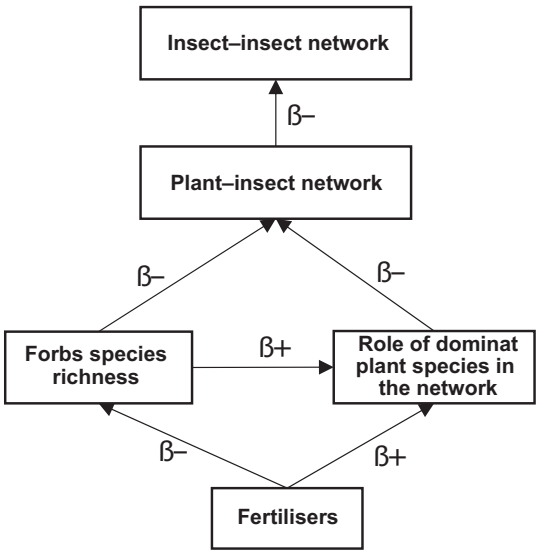

FIGURE 1 Path diagram depicting hypothesised relationships between changes in the plant communities triggered by fertilisation and the networks of interacting species. We expected that fertilisation has a negative effect (β–) on forbs species but a positive effect (β+) on the dominance of some plant species ('winning' species: grasses and *Ranunculus* spp.) which will affect the plant–insect and insect–insect networks. β refers to the mean regression coefficients

degree values attributable to the 'winning' plant species favoured by the fertiliser treatment. We used linear mixed-effects models as explained in Q1. To facilitate model fitting, species richness of the winning plant groups was log(x + 1) transformed, and degree was square root transformed.

3 | RESULTS

In total, 191 species of plant and insect were found in the 72 plots: 34 species of plant (29 forbs and five grasses), 93 species of flower visitors (n = 953), including five species of *Bombus* (n = 52), 32 species of leaf miner (n = 4,614) and 32 species of parasitoid (n = 1,750). On average, and in terms of abundance, we found 13 flower visitors, 64 herbivores and 24 parasitoids per plot. According to the sampling completeness analysis, these data represent 74% of the flower visitors, 97% of the herbivores and 85% of the parasitoid species, estimated for Colt Park Meadows (Table S1). On average, the networks contained 13 species and 32 links (or more specifically: flower-visitor networks had 10 species, leaf miners had 17 species and parasitoid networks had 12 species). The overall network is shown in Figure 2, and a species list is provided in Tables S6–S9.

Q1: Does grassland fertilisation affect the species richness and abundance of plants, flower visitors, leaf miners and parasitoids?

3.1 | Species richness

The number of plant species observed flowering was significantly lower in the NPK + FYM treatment than in the control (27% lower, $p < 0.001$), with no significant difference between the other fertiliser treatments and the control. Insect species richness was unaffected by any of the fertiliser treatments. Although the species richness of neither leaf miners nor parasitoid species was affected by the fertiliser treatments, the number of species of leaf miners attacked by parasitoids was significantly higher with the addition of NPK and NPK + FYM fertilisers, than the control (NPK = 31% higher $p = 0.005$; NPK + FYM = 26% higher $p = 0.043$).

3.2 | Species abundance

The abundance of flowering plant species was significantly lower in the NPK + FYM fertiliser than in the control (46% lower, $p < 0.001$); but there were no differences between the other fertiliser treatments and the control. The abundance of leaf miners and parasitoids was significantly higher in all three fertiliser treatments than in the control (all $p < 0.0001$; Figure S5). The most abundant leaf miners were generalist species that feed on grasses and buttercups (*Ranunculus* spp.), whereas the rarest species were specialists that feed on forbs. The high abundance of leaf miners and parasitoids in fertiliser treatments was mainly due to high numbers of leaf miners feeding on *Ranunculus* spp. For example, *Phytomyza ranunculi* Schrank (Agromyzidae) in particular increased, along with a common parasitoid of agromyzid leaf miners, *Dacnusa laevipectus* Thomson. While the overall abundance of flower visitors was unaffected by the addition of fertilisers ($\chi^2 = 1.92$, $df = 3$, $p = 0.5881$), the abundance of bumblebees declined by 48% when NPK + FYM was added ($p = 0.008$).

Q2: Does grassland fertilisation alter the network of species interactions?

Vulnerability, generality and modularity were all affected by fertilisation to some extent. In comparison to the control, the NPK and NPK + FYM treatments had a significantly higher vulnerability in the flower-visitor networks (i.e. a higher number of flower-visitor species per plant species). Specifically, vulnerability in the NPK treatment was 44% higher ($p = 0.009$), and the NPK + FYM treatments was 39% higher ($p = 0.03$). There was no significant difference in the generality of the flower-visitor network (i.e. there was no difference in the number of plant species visited per flower-visitor species between the fertilised and the control plots). The modularity

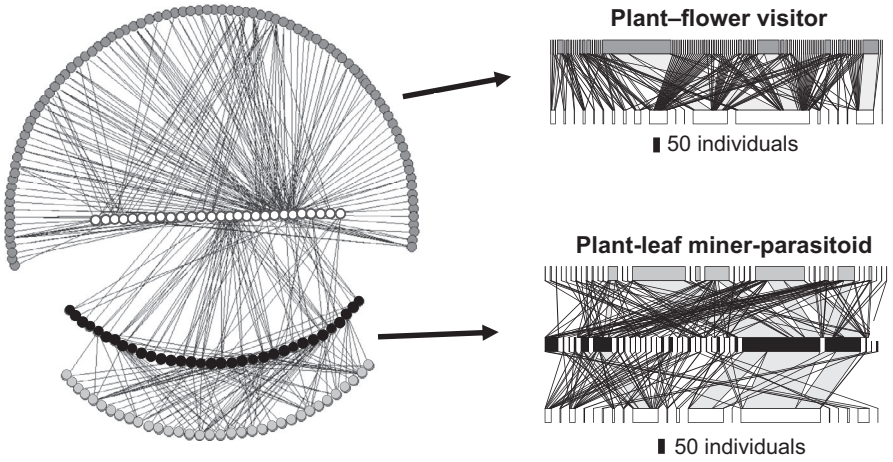

FIGURE 2 The overall network (left) and the plant-flower visitor and plant–herbivore–parasitoid networks shown separately (right) from the Colt Park Meadows experiment. Each square or circle represents a species and lines represent the interactions between them. The overall network is displayed as a qualitative network for ease of presentation, whereas the two constituent webs are shown as quantitative networks. In all three networks, plant species are shown in white, leaf miner species in black, flower visitors in dark grey and parasitoids in light grey

of the network decreased significantly with NPK + FYM, by 34% ($p = 0.003$), and there was a trend with NPK (a 24% reduction, $p = 0.058$).

We observed a similar pattern in the leaf miner network; NPK and NPK + FYM treatments had significantly higher vulnerability, by 20% and 33%, respectively ($p = 0.01$ and $p < 0.001$, respectively), again with no difference in generality ($p > 0.05$). However, the modularity of the networks in the three fertiliser treatments was significantly lower than the control network: NPK by 20% ($p < 0.001$), NPK + FYM by 17.5% ($p = 0.008$) and FYM by 17.6% ($p = 0.001$).

In the leaf miner–parasitoid networks, the NPK and NPK + FYM treatments had a significantly greater generality than the control (i.e. the parasitoids attacked a greater number of leaf miner species; 17% higher, $p = 0.03$ and 25% higher, $p = 0.002$ respectively) but with no difference in vulnerability nor in modularity. Although the leaf miner–parasitoid network in the FYM treatments had a higher vulnerability (23%, $p = 0.03$), there was no difference in generality. Overall, the NPK + FYM treatment impacted the largest number of network metrics.

Q3: What is the relative magnitude of change in the four components of the system, plants, flower visitors, leaf miners and parasitoids, in response to fertilisation?

The impact of the NPK + FYM treatment varied depending on the identity of the group (Figure 3). Thus, while both forb species richness and the abundance of flowers were lower in fertiliser treatments than in the control, the magnitude of these changes as effect sizes (in relation to the variation in the measurements) was small, compared to the increase in leaf miners abundance associated with this shift in plant community structure. The positive impact on the abundance of leaf miners was three times higher than the impact on parasitoids and the negative impact on bumblebee abundance was twice as high as the impact on flower abundance. The negative impact of vulnerability and modularity on flower-visitor networks was twice the magnitude of that seen in the leaf miner networks.

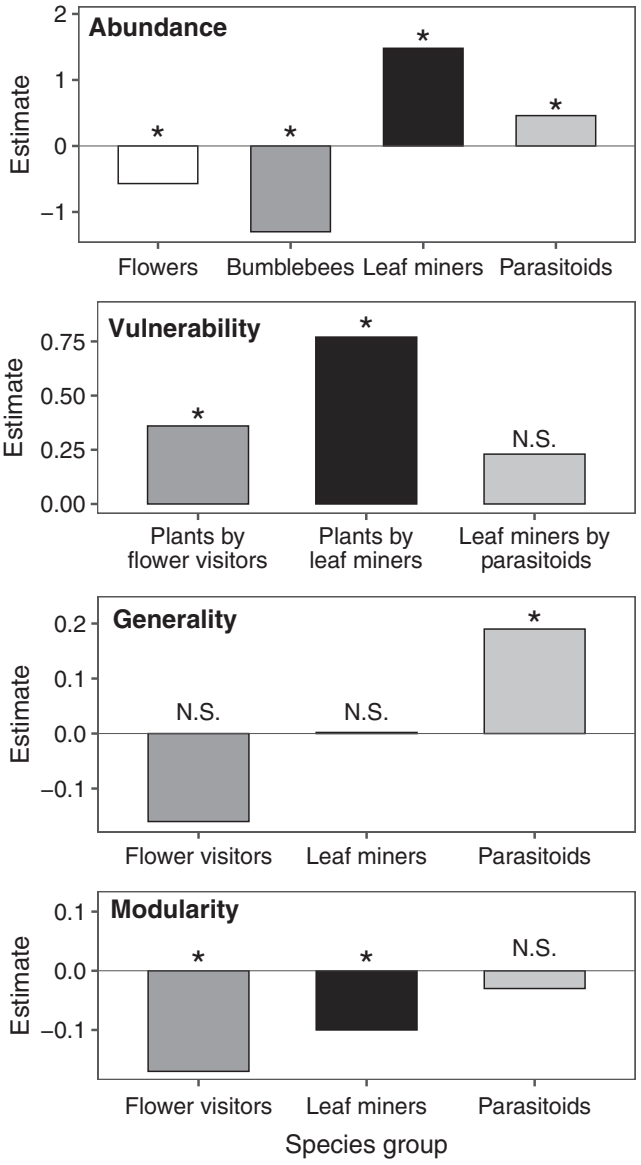

FIGURE 3 The magnitude of the impact of NPK + FYM treatment relative to the control for each insect group. Magnitude was measured as the estimate value calculated from the linear models for abundance, generality, vulnerability and modularity. The asterisk means significant difference and N.S., non-significant

Q4: Are any changes in the network which are attributable to grassland fertilisation, mediated by changes in plant species dominance?

There was higher biomass of perennial grass species in all fertiliser treatments than in the control ($p < 0.001$, Table S2; Figure S2), and greater % cover of *Ranunculus repens* and persistence of its congeneric *R. acris* ($p < 0.001$, Table S2; Figure S3). The total % cover of forbs attributable to *Ranunculus* spp. (*R. repens* L. and *R. acris* L.) was 32% in the control plots and 50% in NPK + FYM (Figure S4). *R. repens* L. and *R. acris* L. were present in all the plots and persisted in the fertilised plots, whereas other forbs became rare (Smith et al., 2008; Figure S2). For our analysis, we combined the two species when considering flower visitors, as we considered it unlikely that pollinators differentiated between them given their similar flower morphology and nectar production (Baude et al., 2016). We confirmed this assumption after finding a similarity of 99% of the flower visitors associated with both species (see Table S3). Similarly, perennial grasses were considered collectively given that they represent a functional group that respond similarly (here positively) to nutrient input (Phoenix et al., 2012; Figure S2) and have a similarity in their associated leaf miners of 77% (see Table S3).

In both plant–flower visitor networks (Figure 4a) and plant–leaf miner–parasitoid networks (Figure 4b), the high vulnerability was mediated by competitively dominant or 'winning' plant species (*Ranunculus* spp. and Grasses respectively). In plant–leaf

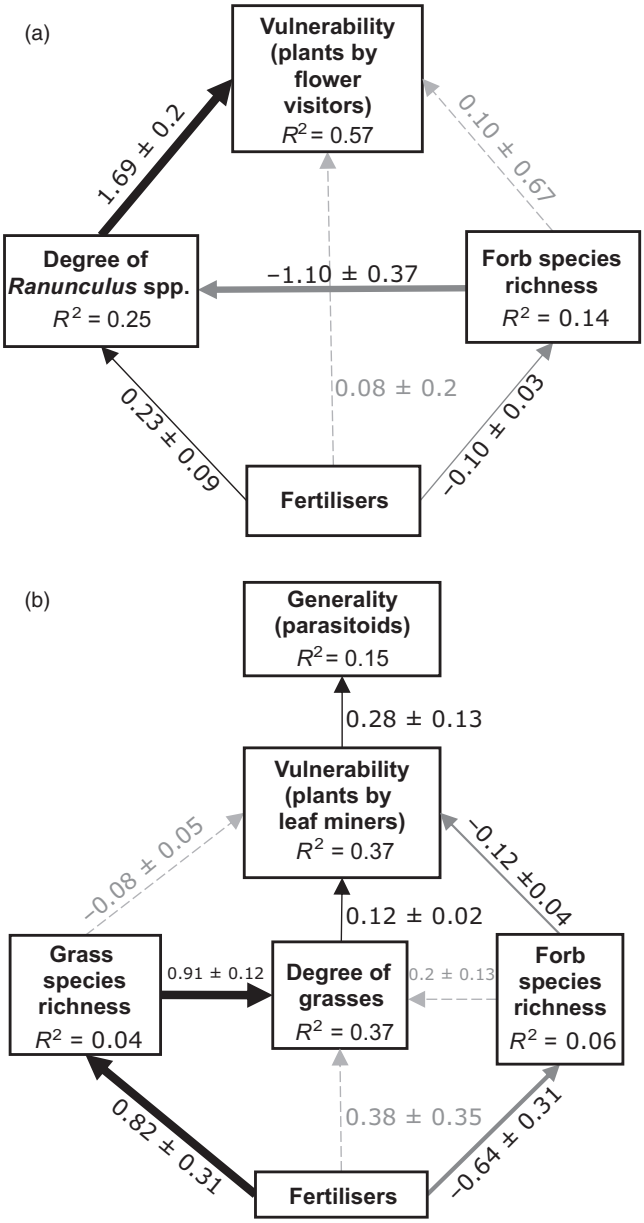

FIGURE 4 Structural modelling graphs, showing the mediating role of dominant plant type on network structure in terms of: (a) Vulnerability of plants in the flower visitor network and (b) Vulnerability of herbivores in the plant–leaf miner network and generality of parasitoids in the leaf miner-parasitoid network. Unstandardised path coefficients are shown with standard errors, and the size of each arrow is proportional to the magnitude of the coefficient. The marginal variance of each model is indicated in the box of the response variable of the model. Positive effects are in black, negative effects in grey. Non-significant paths are indicated with dashed lines

miners–parasitoid networks, such increase was also mediated by low forb species richness (Figure 4b). Specifically, in the flower-visitor networks, the structural equation modelling showed that the low species richness of forb species in the fertiliser treatments resulted in high importance of *Ranunculus* spp. in the network (higher values of the degree metric; $R^2 = 0.25$, $p < 0.05$), leading to higher vulnerability (numbers of insect species per plant species; $R^2 = 0.57$, $p < 0.001$). In the plant–leaf miners network, the higher grass species richness presence driven by the fertiliser treatments resulted in grass species supporting a greater number of observed interactions (higher values of the degree metric; $R^2 = 0.37$, $p < 0.001$). This increase in observed interactions together with the low forb species richness resulted in higher vulnerability (numbers of leaf miners per plant species, $R^2 = 0.37$; $p = 0.001$) that ultimately led to higher generality (number of leaf miner per parasitoid, $R^2 = 0.15$; $p = 0.03$).

4 | DISCUSSION

Our results show that despite insect species richness being unaffected, grassland fertilisation significantly changed community structure, both in terms of species abundance and network structure. There were differences in the magnitude of the effect on the three insect groups: the impact on abundance was highest for the leaf miners, and impact on network structure was highest for flower visitors while the parasitoids network was the least affected. Overall, the fertilised plots had significantly higher leaf miner abundance and parasitoid abundance, but significantly lower flower and bumblebee abundance than the controls. Adding fertiliser changed the vulnerability and modularity of the flower-visitor and leaf miner networks, and the generality of the parasitoid network. There was also a concentration of insect species onto fewer plant resources and a host expansion of parasitoids, where the competitively dominant plant species mediated these changes. In what follows we consider the limitations of our approach and put our results into the context of the wider literature.

4.1 | Limitations

There are two main limitations to our work: (a) While the experiment is long term, our data come from 1 year of sampling and some groups of insects were not sampled (e.g. seed-feeding insects, sap feeding insects, insect predators and decomposers). That said, our study reports on a community of nearly 200 species, and it is the first to consider the differential impact of fertiliser addition on different types of insect networks simultaneously, (b) The size of the plots was small, and they were relatively close to each other and consequently our results correspond to behavioural responses for the pollinator component of the community. However, Orford et al. (2016) demonstrated that plant–pollinator data from small plots predicted farm scale responses for this group, but whether this is the case here remains unknown. Despite these limitations, our main results broadly match the effects of nutrient enrichment on grasslands reported in the literature: loss of forbs species and dominance of species able to capitalise on increased macronutrient availability (Harpole et al., 2016; Phoenix et al., 2012). Further to these results, though, we show that these two changes cascade upwards through the network of species interactions, affecting different guilds of insects and aspects of insect communities in

different ways. Our results do not account for the secondary extinctions that could occur at a larger scale (see Stevens et al., 2018), indeed our results are rather conservative so higher impacts could be expected at a larger scale where impacts on rare species become more detectable. Looking forward field-scale experimental studies are needed to truly assess the impact of fertilisation on insect networks, and to identify the mechanisms through which fertilisers modify network structure.

4.2 | Effects of fertilisers on biological communities

Adding NPK fertilisers with FYM was the most potent driver of change, decreasing the modularity (loss of interacting species groups), increasing the vulnerability of both leaf miners and flower-visitor networks, that is, increasing concentration of animal species on fewer plant species, and the generality of leaf miner–parasitoid networks, that is, increasing number of leaf miner species per parasitoid, whereas adding FYM only increased the vulnerability of the latter and reduced the modularity in leaf miner networks. In the United Kingdom, the use of FYM has been declining in favour of mineral fertilisers resulting in the transformation of 45% of diverse grasslands into agriculturally improved grasslands (Ridding et al., 2015). The smaller impact of FYM compared to NPK on network structure is consistent with the higher biodiversity found with organic farming, in which FYM is commonly used (e.g. Tuck et al., 2014).

In our leaf miner–parasitoid networks, we observed differences between organic and inorganic fertilisers, similar to those reported for cereal crops. Thus, Lohaus et al. (2013) found that aphid–parasitoid networks in organic wheat fields have higher generality and lower vulnerability than those in conventionally farmed wheat fields, despite both having similar numbers of species. However, in their study, the increase in generality was due to a higher number of interactions between aphids and parasitoids. In our NPK treatments, parasitoids expanded their host range to exploit new species. This difference highlights the bottom-up effects of plants on the structure of the third trophic level, as changes in plant community composition ultimately led to a higher generality in the fertilised networks. As demonstrated by the structural equation modelling, leaf miners and flower visitors mainly interacted with the plant species favoured by fertilisation (grasses and *Ranunculus* species). Leaf miners feeding on these become more abundant while visits to *Ranunculus* species by flower visitors increased. However, the abundance of bumblebees was the lowest in plots dominated by grasses and *Ranunculus* spp. The pollen of *Raunculus* is toxic for some bees species (Praz et al., 2008) which suggests that fertilisers not only affect bees by reducing floral resources but also by favouring toxic forb species.

Declines in floral resources following the application of fertiliser have been widely reported (e.g. Phoenix et al., 2012). However, we found that the negative effect of fertilisation on flower abundance was relatively small compared to its negative effect on bumblebee abundance and its positive effect on leaf miner abundance. Contrary to Burkle and Irwin (2009) who reported no change in network structure, we observed that fertilisation did modify plant–flower-visitor network structure at our field sites. We also showed that the effect on flower-visitor networks was much larger than the impact on herbivores networks, despite a higher impact on herbivore abundance. The loss of a species means the loss of interactions and nodes in the network which directly affects its structure. An increase in the abundance of a species, however, changes the frequency of existing interactions, so the impact is more subtle than losing species (Delmas et al., 2019). Thus, a change at one trophic level (here the plant level) can induce differential changes elsewhere in the network.

The dampening effect of fertilisers on parasitoid communities (parasitoids are less affected than the herbivores) contrasts with the escalating impact on pollinators (pollinators are more affected than plants). We observed that parasitoids not only respond to the increase in the abundance of specific leaf miners species (those feeding on *Ranunculus* spp.) but can also feed on other available species, as shown by the attacks on species not recorded in the control plots. Our observations are similar to the results found in experiments of nitrogen deposition and climate change. In those experiments, the replacement of native plants by exotic plants has a greater effect on the biomass of Lepidoptera communities than on their parasitoids which, like ours, changed their host preferences (de Sassi, Lewis, et al., 2012; de Sassi, Staniczenko, et al., 2012; de Sassi & Tylianakis, 2012). Thus, whether the effect of fertilisers are forbs being replaced by grasses (as seen here), or native plants are replaced by alien plants (as reported elsewhere), fertilisers appear to have a differential impact on herbivores and parasitoids.

Although this is the first study that evaluates the relative effect of fertilisation on different insect networks, a number of studies have assessed the effects of land-use intensity on different taxonomic groups including insects (e.g. Kidd et al., 2017; Manning et al., 2015; Simons et al., 2017). These studies report that species groups respond differently, making it hard to use a single species as an indicator. However, those studies only evaluated a single aspect of each community (e.g. species richness) and in some cases, they combined the information of all groups into a single response variable (e.g. Allan et al., 2014) masking differing responses between groups. We not only observed that the groups vary in the direction of their response. We also found a difference in the magnitude of response depending on the variable studied. Moreover, the addition of fertiliser made the insect networks more sensitive to disturbance. The higher dependence of one trophic level, on another, measured as vulnerability and generality, shows a reduction of functional redundancy in the network (Solé & Montoya, 2001). Similarly, the decrease in modularity means that extinction events are more likely to spread within the network (Stouffer & Bascompte, 2011).

In ecological networks, the loss of functional redundancy means that if an extinction occurs, the likelihood that the role of the extinct species can be replaced is reduced, and consequently the probability of secondary extinctions increases (Sanders et al., 2018). Moreover, the rewiring of the generalist species' interactions due to species loss is likely to lead to an increase in competitive interactions (Sanders et al., 2015) and an overexploitation of the remaining

resources (Gilljam et al., 2015), which could lead to further secondary extinctions (i.e. an extinction cascade). In this sense, our results suggest that fertilisation also promotes the loss of species through reducing the functional redundancy and complexity of the networks, which at a larger scale could cause local extinctions.

5 | CONCLUSIONS

Our data highlight the complex effects of fertiliser application on community structure. Thus, we find that the responses of higher trophic levels are affected by non-random plant extinctions, and the magnitude of the effect depends more on the ecology of the species than on species composition per se. However, these results are mainly based on behavioural responses for the pollinator component of the networks given the small scale of the treatment plots. That said, our results are probably rather conservative overall and greater impacts are likely at larger scales. If the bottom-up effects we observed on grassland food webs prove to be widespread, then human actions are not only making the plant communities more functionally similar across habitats (e.g. Smart et al., 2006) but potentially homogenising the structure of associated invertebrate networks. A question which remains to be answered is to quantify the relationship between network response and the ensuing effect on ecosystem services such as pest control and pollination. In essence, do these network changes influence the ecological functions delivered for free by nature? If we are to truly understand the impact of fertilisers on community structure and function, then considering multiple networks simultaneously are likely to reveal new ecological patterns, along with highlighting new priorities and new approaches for mitigating negative effects. Moreover, studying the ecological mechanisms through which human actions affect the food web structure can significantly increase our understanding of the factors affecting the structure and function of both natural and managed communities.

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AUTHORS' CONTRIBUTIONS

J.M. conceived the main idea; E.V.-G. conducted the sampling and analysis, the latter with assistance from S.M.S.; S.M.S. and S.E.W. helped with field logistics and analysis; E.L.C. and E.V.-G. conducted the bioinformatic analysis; E.V.-G. wrote the manuscript with input from J.M. and S.M.S. All authors assisted with revisions.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.vmcvdncr3 (Villa-Galaviz et al., 2020).

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SUPPORTING INFORMATION

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

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