1   **The robustness and restoration of a network of ecological networks**

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16   1 sentence summary. The robustness of linked networks in an agroecosystem vary but do not

17   strongly co-vary.

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Understanding species' interactions and the robustness of interaction networks to species loss is essential to understand the effects of species' declines and extinctions. In most studies, different types of network (e.g food webs, parasitoid webs, seed dispersal networks and pollination networks) have been studied separately. We sampled such multiple networks simultaneously in an agroecosystem. We show that the networks varied in their robustness; networks including pollinators appeared particularly fragile. We show that, overall, networks did not strongly co-vary in their robustness suggesting that ecological restoration, e.g. through agri-environmental schemes, benefitting one functional group will not inevitably benefit others. Some individual plant species were disproportionately well-linked to many other species. This type of information can be used in restoration management as it identifies the plant taxa which potentially lead to disproportionate gains in biodiversity.

All species are embedded in complex networks of interactions (*1*). Modeling food webs, and more generally, species' interaction networks, has advanced the understanding of the robustness of ecosystems in the face of species loss (*1, 2*). A key question, of applied relevance, is how the robustness of different species' interaction networks varies and whether it co-varies. This is particularly important given the current rate of species' declines and extinctions (*3*) and its consequent impact on ecosystem function. Currently, understanding of species' interaction networks is mostly limited to partial subsets of whole ecosystems (but see (*4, 5*)). However, studying the interdependence of different networks is important (*6*) and can alter our perspective of network fragility, a fact already shown with non-ecological examples (*7*). Moreover, this approach can be used to identify keystone species in the overall network;

43   if these species were the focus of restoration effort then disproportionate gains for

44   biodiversity are a real possibility.

45   Here, we have overcome the logistical constraints of studying multiple species'

46   interaction networks in order to more fully test for variation in their robustness and fragility.

47   Our networks comprised 1501 quantified unique interactions between a total of 560 taxa,

48   comprising plants and 11 groups of animals: those feeding on plants (butterflies and other

49   flower visitors, aphids, seed-feeding insects, and granivorous birds and mammals) and their

50   dependants (primary and secondary aphid parasitoids, leaf miner parasitoids, parasitoids of

51   seed-feeding insects and rodent ectoparasites) (Fig. 1). We selected these groups because

52   sampling their interactions is tractable in the field, they encompass a wide taxonomic and

53   functional range, and they include animals regarded as bioindicators, e.g. birds and butterflies

54   *(8, 9)*, and as ecosystem service providers, e.g. pollinators and parasitoids (*10*, *11*) (table S1).

55   The networks thus included trophic (*12*), mutualistic (*13*) and parasitic (*4*) interactions.

56   Previously these networks have only been studied in isolation because they are logistically

57   difficult to sample and because most terrestrial ecologists focus on only a taxonomic subset

58   of species (e.g. birds, butterflies or bumblebees).

59   We worked at the whole-farm scale on a 125 ha farm (Norwood Farm, Somerset,

60   UK), and undertook replicated sampling in all habitats, both cropped and non-cropped over

61   two years (*14*). The abundance of each of the 560 taxa was quantified from field surveys.

62   Interaction frequencies in most networks were quantified directly from field sampling (and

63   thus represent a sample of each taxon's realised niche). Logistical constraints stopped us from

64   identifying leaf-mining insects, so leaf-miner parasitoids were treated as if they were linked

65   directly to host plants (thus assuming them to be generalist on leaf-miners that were host-

66   specific; an approach justified in (*14*)). For birds, mammals and butterflies, their interactions

67   with plants were based on prior knowledge of their interactions (from the literature) and were

68   quantified with models of foraging behavior (details in (*14*); and thus approximated the

69   taxon's realised niche). Intensive study of a single site, as in many other food web studies,

70   e.g. (*15, 16*), provided us with spatio-temporal replication across habitats and seasons, and

71   detailed data that we could not have obtained from extensive surveys of multiple farms. We

72   sampled this particular farm because we expected it to be relatively biodiverse (it was

73   managed organically at relatively low intensity, and was subject to an agri-environmental

74   scheme). This allowed us to simulate species loss from a biodiverse site, which provided

75   stronger inference than if we had simulated the gain of (by definition, unrecorded) species

76   from a low diversity site.

77   We evaluated the robustness of 11 groups of animals, comprising each trophic level in

78   the seven linked networks, by simulating the sequential removal of plant taxa 20 000 times

79   (*14*). In our model, animal taxa became disconnected (a 'secondary extinction') when all their

80   food species became extinct; depending on the animal group this was either plants or the

81   animals they preyed upon. In simulating the loss of plants, we used an established method

82   (*12, 17*), and assumed bottom-up rather than top-down regulation of the animals, as justified

83   by (*18*). This ecologically-informed approach has practical application because plants can be

84   managed more directly (e.g. through field rotations or via agri-environment schemes (*19*))

85   than putative animal bioindicators. We considered two complementary models of robustness:

86   where all taxa were weighted equally, (R_S) (*17*) and the quantitative equivalent, where taxa

87   are weighted by their abundance (R_Q) (*20*), calculating R as the average area under the curve

88   of the secondary extinctions against primary extinctions across the 20 000 simulations (*21*).

89   Given this approach, our models can be interpreted equally as representing the cascading

90   negative effects of plant loss and the cascading positive effects of plant restoration.

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91   We found that under randomized sequences of loss of plant taxa, the bird seed-feeder,

92   rodent seed-feeder, rodent ectoparasite and secondary aphid parasitoid networks were most

93   robust ($R \rightarrow 1$; Fig. 2). The robustness of the first two networks were derived from literature-

94   based interactions so they represent the entire realised niche rather than a sample of the

95   realised niche, while the third depended on a network derived from literature-based

96   interactions. However, all of our reported conclusions are robust to the exclusion of

97   literature-derived networks and to variation in sampling efficiency (SOM Part 5; tables S4

98   and S7). Aphid, insect-seed feeder and pollinator networks appeared more fragile ($R \rightarrow 0.5$;

99   Fig. 2). We tested whether robustness was related to other network metrics (table S4). We

100 found that network robustness was related to network generalisation (the relationship of H_2',

101 a measure of niche differentiation (*22, 23*), to R_S: β=-0.903, t_9=-2.316, P=0.046, and to R_Q:

102 β=-0.545, t_9=-6.131, P< 0.001). We also found that network robustness was not related to

103 network complexity (the relationship of e^{H_2}, a measure of interaction diversity (*22, 23*), to

104 R_S: β=0.018, t_9=0.231, P=0.823, and to R_Q: β=0.099, t_9=1.769, P=0.111). Our findings

105 provide no positive support for the long-debated relationship between complexity and

106 stability, in common with other empirical studies (*24*). The relationship of robustness with

107 generalization is likely to be explained through the nestedness that is characteristic of many

108 ecological networks, and which confers robustness to networks (*24, 25*).

109 Although the animals in the networks all depended (directly or indirectly) on plant

110 taxa, we found that the robustness of some networks co-varied, but overall the covariance

111 was less than expected compared to a null model (Fig. 3; SOM Part 3). Importantly, none of

112 the correlations was substantially negative (min *r*=-0.05; table S5), so sequences of plant loss

113 that were relatively benign for one animal group were never consistently unfavorable for

114 another group. Although some individual pairwise correlations were strongly positive (Fig.

3E, F), these correlations were between animal groups that were linked either trophically (e.g.

fleas and rodents) or through shared resources (e.g. butterflies and seed-feeding insects which

shared plant hosts). The practical implication of these findings to our agroecosystem is that

agri-environmental management of plants that is targeted to produce cascading positive

effects for one animal group (e.g. farmland insect pollinators) will have varying (but not

systematically negative) effects on other animal groups. Such results have indeed been found

with empirical assessments of agri-environmental scheme success more generally (*26*).

Our approach, considering the robustness of the linked networks, provides

information on the network of networks. To reveal the varying importance of individual

species within these linked networks, we identified the most important plants within the

networks, i.e. 'keystone' (*27*) plant taxa that have substantial and disproportionate cascading

effects across the multiple networks (Fig. 4). In practical terms, this information could be

used to focus restoration management on plant taxa with the greatest potential to achieve

efficient and positive results for biodiversity and their resultant ecosystem services. We found

that the taxa that were most important relative to their abundance (i.e. had most influence on

modelled robustness across the networks (*14*)) tended to: (i) be non-woody taxa; (ii) occur in

non-cropped ground; and (iii) be members of the Apiaceae and Asteraceae families (Fig. 4,

table S6, fig. S3). Agri-environmental policies encouraging plants with high relative

importance could provide benefits for biodiversity, and so potentially support ecosystem

service provision, but because some of these plants are typically regarded as farmland weeds

this could be controversial. Any such policies would need to consider how these relationships

are affected by local farming system and landscape context (*28*), and would need to consider

the balance of practicality (how these plants are affected by agricultural practice, including

arable crop rotations), cost (impacts on crop yield/profitability and detrimental effects on rare

139 farmland plants of conservation concern) as well as the benefits (cascading effects on

140 biodiversity and, potentially, ecosystem services).

141 Agricultural change has been one of the main drivers of biodiversity loss in recent

142 times (*29*), and yet during this period the importance of ecosystem services provided by

143 biodiversity, even in intensive agricultural systems, has become well recognized (*30*). Our

144 approach, which included empirically constructing multiple, linked networks for cropped and

145 semi-natural habitat at a whole farm extent, and modeling their response to environmental

146 change could become increasingly important for research on biodiversity and ecosystem

147 services. The optimist's scenario, of management targeted to benefit one animal group but

148 resulting in multiple benefits for many different groups, was not supported by our modeling

149 of empirical species' interaction data from this site. Therefore, in order to bring benefits to a

150 wide range of taxa, it is essential to have focused and ecologically-informed management,

151 e.g. the targeted management of specific plant taxa based on their cascading effects with a

152 network of networks.

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228   **Supporting Online Material**

229   Materials and Methods

230   Tables S1-5

231   Figs S1-3

232   SOM Text: Full acknowledgements

233   References ($1 - 80$)

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Figures

Fig. 1. Species' interaction networks for Norwood Farm, Somerset, UK. The entire network of networks is shown top left (in which each circle represents one species) and quantitative visualisations are shown for each of the seven quantified individual networks (in which each block is a species and the width of blocks of each colour represent relative abundance). Details of the networks are given in table S1 and (*14*). Bright green and light green circles and blocks indicate non-crop and crop plants, respectively, while other colours indicate animal groups. Scale bars indicate the abundance of animal taxa. Plants are scale in proportion to their interactions with animals in each network.

Fig. 2. The average robustness of the 11 animal groups (median ($\bar{R}$) ± 90 percentiles). The coloured bars, matching colours in Fig. 1, show R_S and the adjoining white bars show R_S. As $\bar{R} \to 1$, animal groups are increasingly robust to the simulated sequential loss of plant taxa, while for animal groups with low robustness $\bar{R} \to 0.5$.

Fig. 3. Correlations between the robustness of animal groups and the simulated loss of plant taxa in networks of the farmland species' interaction network. The robustness of flower visitors to one random sequence of plant loss is the area under the curve for (**A**) the qualitative case and (**B**) the quantitative case. The pairwise correlations in robustness varied in the 20 000 simulations of the sequential loss of plant taxa, as two examples (**C, D**) show. These pairwise correlations were summarised to show the connectivity between all animal groups, considering (**E**) R_S and (**F**) R_Q.

Fig. 4. The relative importance of the plants in the Norwood Farm network of quantified networks. (**A**) The relative importance of the plants varied by habitat with colours from white to red representing increasing abundance, as shown in (**G**), and was calculated as shown in this workflow (**B-G**). The importance of each species of plant (*j*) for each animal group (*i*) was the coefficient of determination (r_{ij}^2), i.e. the square of the correlation coefficient, between the calculated robustness with plants removed in random order and the position of the plant in that order, as exemplifed for (**B**) *Rubus fruticosus* and butterflies, (**C**) *Anthriscus sylvestris* and flower visitors, (**D**) *Persicaria* spp. and birds,

261   and (**E**) *Anthriscus sylvestris* and leafminer parasitoids. (**F**) The weighted sums of these coefficient of

262   determinations across groups (*g*) gave the importance (*I*) of each plant taxon; in this case the groups

263   were weighted their uniqueness (SOM Part 4). (**G**) Abundance (assessed as leaf area of the plants (*14*,

264   *31*)) was strongly related to importance for a subset of plant taxa, so the relative importance of each

265   plant taxon (*RI*) was calculated as the residual from the steeper regression line (determined by a two-

266   component mixture regression model), exemplifed by *Cirsium vulgare* (*Cv*), *Anthriscus sylvestris* (*As*)

267   and *Hordeum vulgare* (*Hv*).

268

269   Fig. 1

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Flower - flower visitor

10^4

Flower - butterfly

10^2

Plant - aphid - aphid parasitoid

Primary aphid parasitoid   Secondary aphid parasitoid

10^6

10^7

Plant - leaf-miner parasitoid

10^6

Seed - granivorous bird

10^1

Seed - insect seed-feeder - parasitoid

10^5

10^5

Seed - rodent - ectoparasite

10^1

10^1

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271   Fig. 2

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277   Fig. 4

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