Article (refereed) - postprint

Pocock, Michael J.O.; Evans, Darren, M.; Memmott, Jane. 2012 The robustness and restoration of a network of ecological networks. *Science*, 335 (6071). 973-977. 10.1126/science.1214915

The robustness and restoration of a network of ecological networks

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

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;

if these species were the focus of restoration effort then disproportionate gains for biodiversity are a real possibility.

Here, we have overcome the logistical constraints of studying multiple species' interaction networks in order to more fully test for variation in their robustness and fragility. Our networks comprised 1501 quantified unique interactions between a total of 560 taxa, comprising plants and 11 groups of animals: those feeding on plants (butterflies and other flower visitors, aphids, seed-feeding insects, and granivorous birds and mammals) and their dependants (primary and secondary aphid parasitoids, leaf miner parasitoids, parasitoids of seed-feeding insects and rodent ectoparasites) (Fig. 1). We selected these groups because sampling their interactions is tractable in the field, they encompass a wide taxonomic and functional range, and they include animals regarded as bioindicators, e.g. birds and butterflies *(8, 9)*, and as ecosystem service providers, e.g. pollinators and parasitoids (*10, 11*) (table S1). The networks thus included trophic (*12*), mutualistic (*13*) and parasitic (*4*) interactions. Previously these networks have only been studied in isolation because they are logistically difficult to sample and because most terrestrial ecologists focus on only a taxonomic subset of species (e.g. birds, butterflies or bumblebees).

We worked at the whole-farm scale on a 125 ha farm (Norwood Farm, Somerset, UK), and undertook replicated sampling in all habitats, both cropped and non-cropped over two years (*14*). The abundance of each of the 560 taxa was quantified from field surveys. Interaction frequencies in most networks were quantified directly from field sampling (and thus represent a sample of each taxon's realised niche). Logistical constraints stopped us from identifying leaf-mining insects, so leaf-miner parasitoids were treated as if they were linked directly to host plants (thus assuming them to be generalist on leaf-miners that were host-specific; an approach justified in (*14*)). For birds, mammals and butterflies, their interactions with plants were based on prior knowledge of their interactions (from the literature) and were quantified with models of foraging behavior (details in (*14*); and thus approximated the taxon's realised niche). Intensive study of a single site, as in many other food web studies, e.g. (*15, 16*), provided us with spatio-temporal replication across habitats and seasons, and detailed data that we could not have obtained from extensive surveys of multiple farms. We sampled this particular farm because we expected it to be relatively biodiverse (it was managed organically at relatively low intensity, and was subject to an agri-environmental scheme). This allowed us to simulate species loss from a biodiverse site, which provided stronger inference than if we had simulated the gain of (by definition, unrecorded) species from a low diversity site.

We evaluated the robustness of 11 groups of animals, comprising each trophic level in the seven linked networks, by simulating the sequential removal of plant taxa 20 000 times (*14*). In our model, animal taxa became disconnected (a 'secondary extinction') when all their food species became extinct; depending on the animal group this was either plants or the animals they preyed upon. In simulating the loss of plants, we used an established method (*12, 17*), and assumed bottom-up rather than top-down regulation of the animals, as justified by (*18*). This ecologically-informed approach has practical application because plants can be managed more directly (e.g. through field rotations or via agri-environment schemes (*19*)) than putative animal bioindicators. We considered two complementary models of robustness: where all taxa were weighted equally, (R_S) (*17*) and the quantitative equivalent, where taxa are weighted by their abundance (R_Q) (*20*), calculating $\overline{R}$ as the average area under the curve of the secondary extinctions against primary extinctions across the 20 000 simulations (*21*). Given this approach, our models can be interpreted equally as representing the cascading negative effects of plant loss and the cascading positive effects of plant restoration.

We found that under randomized sequences of loss of plant taxa, the bird seed-feeder, rodent seed-feeder, rodent ectoparasite and secondary aphid parasitoid networks were most robust ($\bar{R} \to 1$; Fig. 2). The robustness of the first two networks were derived from literature-based interactions so they represent the entire realised niche rather than a sample of the realised niche, while the third depended on a network derived from literature-based interactions. However, all of our reported conclusions are robust to the exclusion of literature-derived networks and to variation in sampling efficiency (SOM Part 5; tables S4 and S7). Aphid, insect-seed feeder and pollinator networks appeared more fragile ($\bar{R} \to 0.5$; Fig. 2). We tested whether robustness was related to other network metrics (table S4). We found that network robustness was related to network generalisation (the relationship of H_2', a measure of niche differentiation (*22, 23*), to R_S: β=-0.903, t_9=-2.316, P=0.046, and to R_Q: β=-0.545, t_9=-6.131, P< 0.001). We also found that network robustness was not related to network complexity (the relationship of e^{H_2}, a measure of interaction diversity (*22, 23*), to 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 provide no positive support for the long-debated relationship between complexity and stability, in common with other empirical studies (*24*). The relationship of robustness with generalization is likely to be explained through the nestedness that is characteristic of many ecological networks, and which confers robustness to networks (*24, 25*).

Although the animals in the networks all depended (directly or indirectly) on plant taxa, we found that the robustness of some networks co-varied, but overall the covariance was less than expected compared to a null model (Fig. 3; SOM Part 3). Importantly, none of the correlations was substantially negative (min r=-0.05; table S5), so sequences of plant loss that were relatively benign for one animal group were never consistently unfavorable for 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 farmland plants of conservation concern) as well as the benefits (cascading effects on biodiversity and, potentially, ecosystem services).

Agricultural change has been one of the main drivers of biodiversity loss in recent times (*29*), and yet during this period the importance of ecosystem services provided by biodiversity, even in intensive agricultural systems, has become well recognized (*30*). Our approach, which included empirically constructing multiple, linked networks for cropped and semi-natural habitat at a whole farm extent, and modeling their response to environmental change could become increasingly important for research on biodiversity and ecosystem services. The optimist’s scenario, of management targeted to benefit one animal group but resulting in multiple benefits for many different groups, was not supported by our modeling of empirical species’ interaction data from this site. Therefore, in order to bring benefits to a wide range of taxa, it is essential to have focused and ecologically-informed management, e.g. the targeted management of specific plant taxa based on their cascading effects with a network of networks.

References and Notes

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Acknowledgements: Jo Brooks helped throughout the project and fourteen field assistants helped with field and laboratory work; 15 taxonomists (listed in SOM text) assisted with species' identification; Cate Le Grice-Mack (the landowner) gave full support throughout the project. The authors declare no competing interests. The interaction data is available from:

doi:10.5061/dryad.3s36r118. The project was supported by the Biotechnology and Biological Sciences Research Council [grant number BBD0156341].

Supporting Online Material

Materials and Methods

Tables S1-5

Figs S1-3

SOM Text: Full acknowledgements

References (*1 – 80*)

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 $\bar{R} \rightarrow 1$, animal groups are increasingly robust to the simulated sequential loss of plant taxa, while for animal groups with low robustness $\bar{R} \rightarrow 0.5$.

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,

and (**E**) *Anthriscus sylvestris* and leafminer parasitoids. (**F**) The weighted sums of these coefficient of determinations across groups (*g*) gave the importance (*I*) of each plant taxon; in this case the groups were weighted their uniqueness (SOM Part 4). (**G**) Abundance (assessed as leaf area of the plants (*14*, *31*)) was strongly related to importance for a subset of plant taxa, so the relative importance of each plant taxon (*RI*) was calculated as the residual from the steeper regression line (determined by a two-component mixture regression model), exemplifed by *Cirsium vulgare* (*Cv*), *Anthriscus sylvestris* (*As*) and *Hordeum vulgare* (*Hv*).

Fig. 1

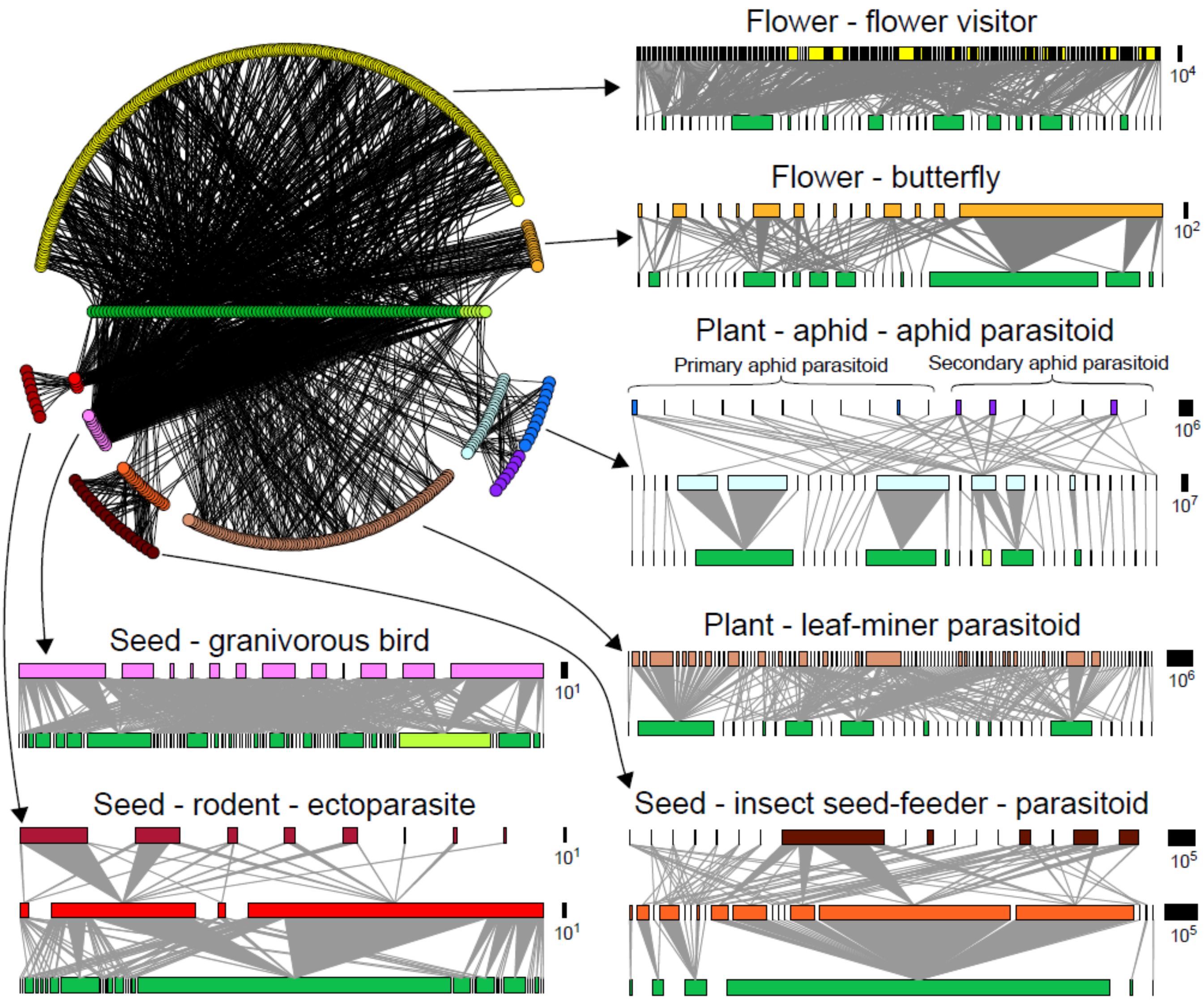

Flower - flower visitor
10^4
Flower - butterfly
10^2
Plant - aphid - aphid parasitoid
Primary aphid parasitoid
Secondary aphid parasitoid
10^6
10^7
Seed - granivorous bird
10^1
Plant - leaf-miner parasitoid
10^6
Seed - rodent - ectoparasite
10^1
10^1
Seed - insect seed-feeder - parasitoid
10^5
10^5

Fig. 2

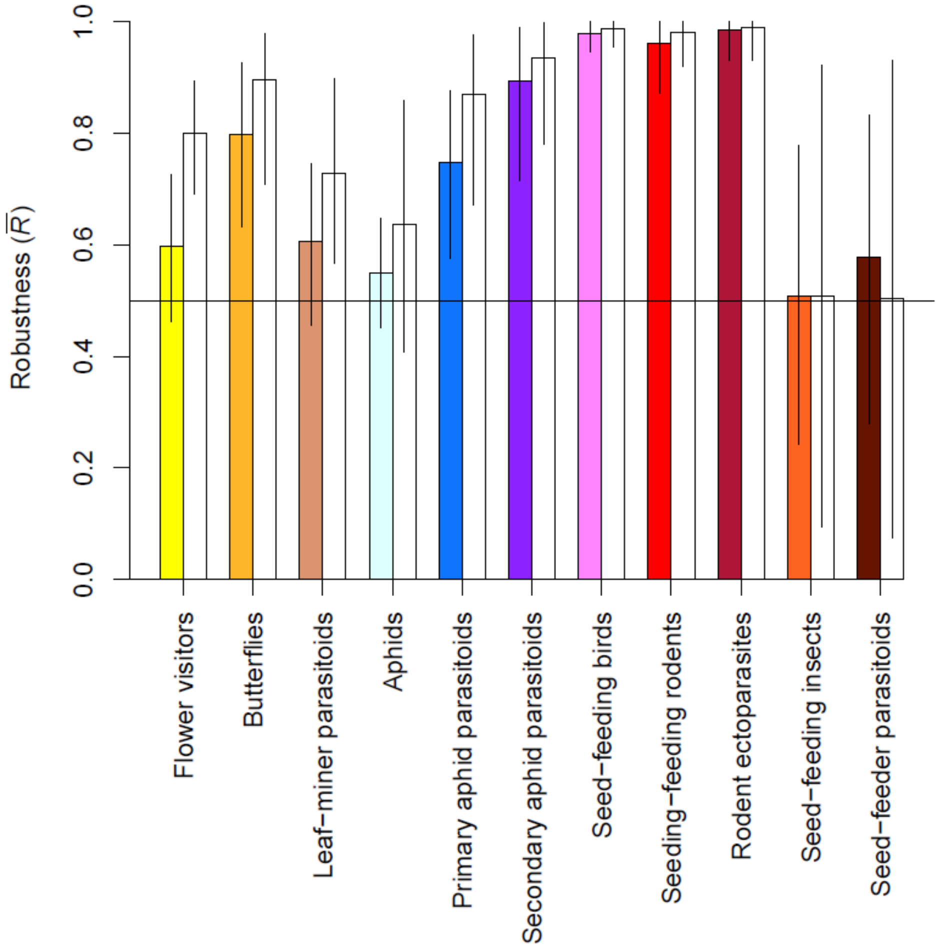

Robustness ($\overline{R}$)
0.0
0.2
0.4
0.6
0.8
1.0
Flower visitors
Butterflies
Leaf–miner parasitoids
Aphids
Primary aphid parasitoids
Secondary aphid parasitoids
Seed–feeding birds
Seeding–feeding rodents
Rodent ectoparasites
Seed–feeding insects
Seed–feeder parasitoids

Fig. 3

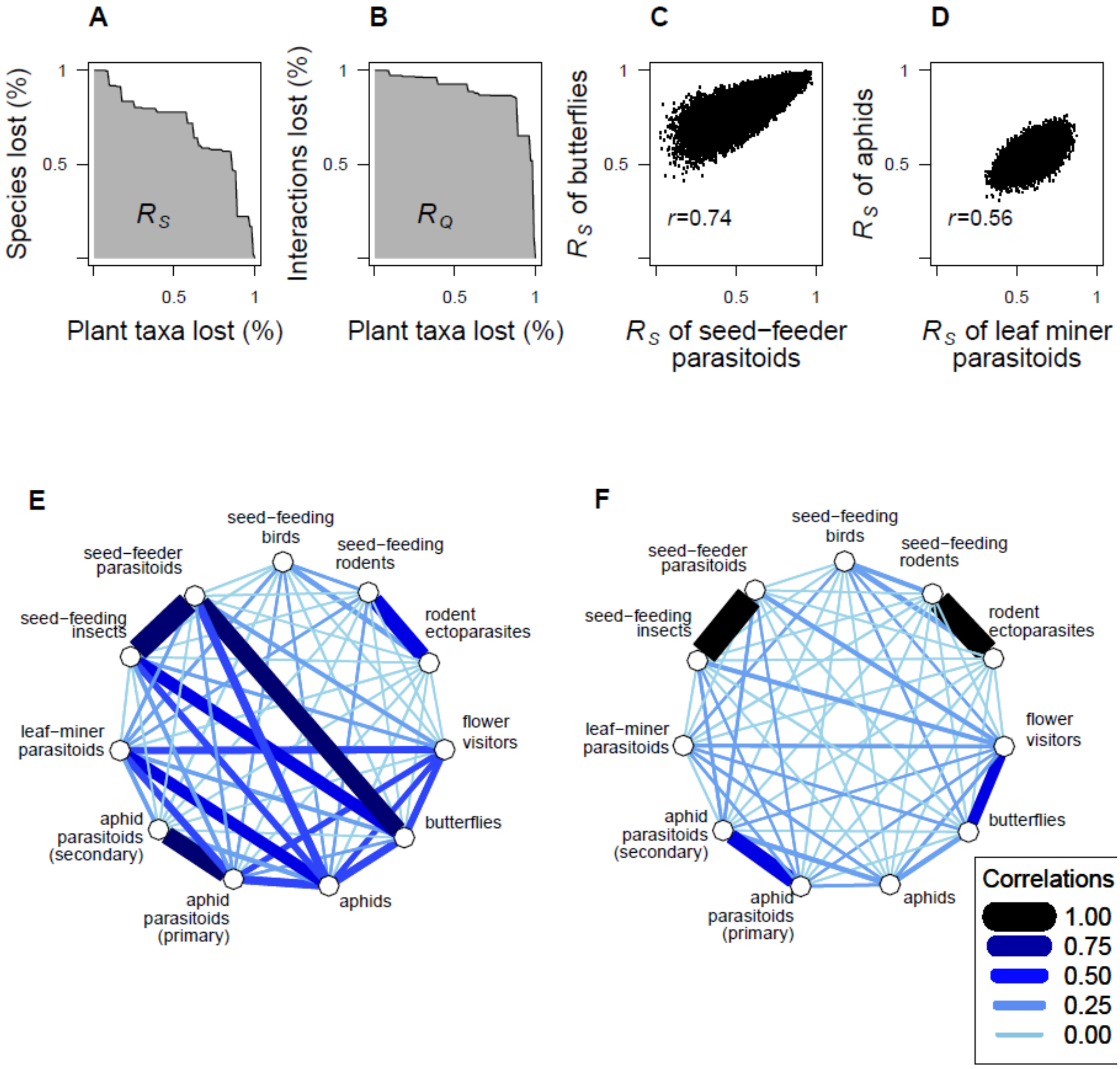
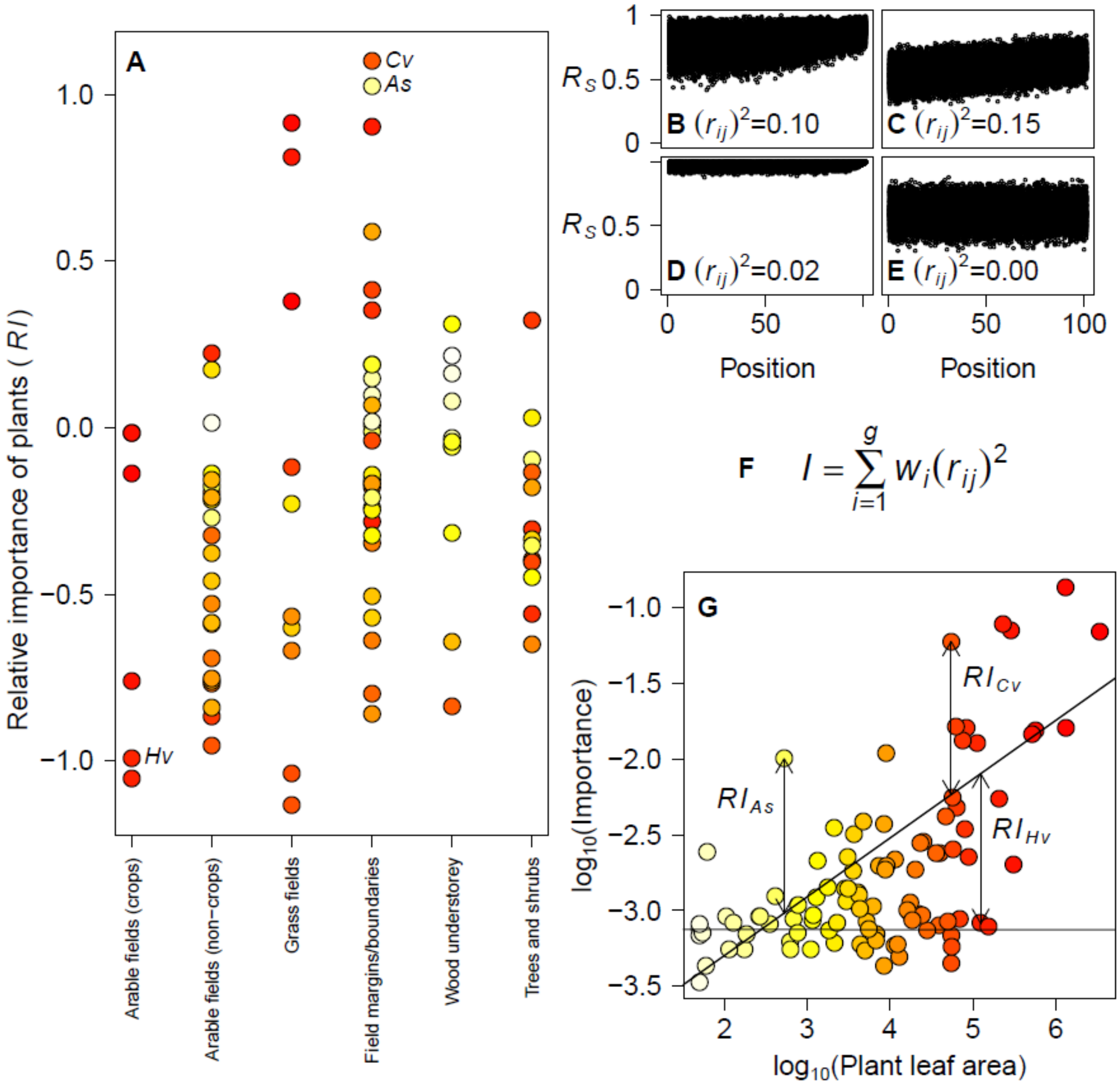

A
Species lost (%)
R_S
Plant taxa lost (%)
B
Interactions lost (%)
R_Q
Plant taxa lost (%)
C
R_S of butterflies
r=0.74
R_S of seed−feeder parasitoids
D
R_S of aphids
r=0.56
R_S of leaf miner parasitoids
1
0.5
E
F
seed−feeding birds
seed−feeding rodents
rodent ectoparasites
flower visitors
butterflies
aphids
aphid parasitoids (primary)
aphid parasitoids (secondary)
leaf−miner parasitoids
seed−feeding insects
seed−feeder parasitoids
Correlations
1.00
0.75
0.50
0.25
0.00

Fig. 4


A
Cv
As
Hv
1.0
0.5
0.0
−0.5
−1.0
Relative importance of plants (RI)
Arable fields (crops)
Arable fields (non−crops)
Grass fields
Field margins/boundaries
Wood understorey
Trees and shrubs
R_S
1
0.5
0
B $(r_{ij})^2$=0.10
C $(r_{ij})^2$=0.15
D $(r_{ij})^2$=0.02
E $(r_{ij})^2$=0.00
0
50
100
Position
Position
F $I = \sum_{i=1}^{g} w_i (r_{ij})^2$
G
RI_{Cv}
RI_{As}
RI_{Hv}
−1.0
−1.5
−2.0
−2.5
−3.0
−3.5
$\log_{10}$(Importance)
2
3
4
5
6
$\log_{10}$(Plant leaf area)