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The robustness of a network of ecological networks to habitat loss

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ABSTRACT

There have been considerable advances in our understanding of the tolerance of species interaction networks to sequential extinctions of plants and animals. However, communities of species exist in a mosaic of habitats, and the vulnerability of habitats to anthopogenic change varies. Here we model the cascading effects of habitat loss, driven by plant extinctions, on the robustness of multiple animal groups. Our network is constructed from empirical observations of 11 animal groups in twelve habitats on farmland. We simulated sequential habitat removal scenarios: randomly; according to prior information; and with a genetic algorithm to identify best- and worst-case permutations of habitat loss. We identified two semi-natural habitats (waste ground and hedgerows together comprising <5% of the total area of the farm) as disproportionately important to the integrity of the overall network. Our approach provides a new tool for network ecologists and for directing the management and restoration of multiple-habitat sites.

INTRODUCTION

The past decade has seen significant advances in the theoretical understanding, construction, analysis and application of complex species interactions networks (see Fontaine *et al.* 2011; Kefi *et al.* 2012 for reviews). Ecological networks describe the interactions between species, the underlying structure of communities and the function and stability of ecosystems (Montoya *et al.* 2006). They have the potential to quantify the effects of human activities on a wide range of complex ecological interactions (Memmott *et al.* 2007; Tylianakis *et al.* 2008). Of the numerous ecological network properties, network 'robustness' (a measure of the tolerance of the network to species extinctions (Dunne *et al.* 2002; Memmott *et al.* 2004)) has received particular attention, partly driven by advances in computational modelling (Kaiser-Bunbury *et al.* 2010; Staniczenko *et al.* 2010), but mostly by the desire to understand the real threat of biodiversity loss to ecosystem services and functioning (Pocock *et al.* 2012). Our understanding of network robustness to species loss has thus advanced from studies of simple qualitative, bipartite mutualistic networks (Memmott *et al.* 2004), to investigations of patterns across ecosystems (Srinivasan *et al.* 2007) and to current quantitative approaches that take into account species abundance (Kaiser-Bunbury *et al.* 2010).

Despite these advances, few studies have considered the robustness of complex ecological networks to habitat loss. Habitat destruction is the primary cause of biodiversity loss (Pimm & Raven 2000) and arguably a more common ecological scenario than species extinction cascades. The impacts of habitat management (effectively habitat addition, loss and change) are likely to have large cascading effects within ecological networks, as they will simultaneously affect multiple species across trophic levels (see Tylianakis *et al.* 2008 for review of global change impacts). Moreover, there has been a paradigm shift in conservation policy away from targeting single vulnerable species to managing entire communities, especially if they provide benefits to humans (Millennium Ecosystem Assessment 2005).

Practically, conservation effort is habitat-focussed whether restoring local degraded water-bodies, or implementing continent-wide agri-environment schemes (Tscharntke *et al.* 2005). While the theoretical consequences of habitat loss (typically a reduction in area of a given habitat) has been considered in ecological network analysis (Melian & Bascompte 2002; Fortuna & Bascompte 2006), the impact of the loss of particular components of habitat heterogeneity has not. For example: what would be the network-level effects of the loss of creeks due to water abstraction in desert systems, or of a farmer removing hedgerows to maximise production? In this study, we test the robustness of multiple species-interaction networks to simulated habitat loss. Our focus is on species-interaction networks within an agro-ecosystem. We chose this environment because: low-intensity farmland is often comprised of multiple, distinct habitats occurring in a landscape-level mosaic; sampling multiple farmland species interactions is tractable in the field (Van Veen *et al.* 2008; Macfadyen *et al.* 2009; Evans *et al.* 2011); European farms tend to have high habitat heterogeneity (Benton *et al.* 2003) and the intensity of management between the habitats can differ markedly (i.e. unmanaged woodland to intensively managed annual crops); farmland animals and plants encompass animals regarded as bioindicators, e.g. birds and butterflies (McGeoch 1998; Anon. 2010), and as ecosystem service providers, e.g. pollinators and parasitoids (Losey & Vaughan 2006; Sandhu *et al.* 2008); and meeting the world’s future food security needs, whilst maintaining and enhancing biodiversity, is of major policy relevance (Sutherland *et al.* 2009).

Our objectives are fourfold: 1) To test the robustness of a farm-scale network of ecological networks to random habitat loss, i.e. the loss of suites of habitat-specific species interactions. We predict that groups within the network will be vulnerable to habitat loss if there are a high number of habitat-specific interactions; 2) To quantify the importance of each habitat within the network. Previously we determined the importance of each plant species in the network (Pocock *et al.* 2012). Here, we apply an analogous approach for each habitat; 3) To examine how similar habitats are in terms of shared species and whether this and/or biodiversity “spill-over” (Brudvig *et al.* 2009) between habitats affects robustness. If the similarity of plants and associated animals between habitats is high, then we predict that the robustness of the animal groups to habitat loss will be high due to a low number of habitat-specific interactions; 4) To determine the best and worst-case permutations for the order in which habitat type is lost using a genetic algorithm and to compare these three with habitat loss scenarios based on habitat management intensity (a reasonable, albeit subjective, approach) as well as measures of plant similarity and habitat importance. These four objectives collectively will enable us to identify the most important habitats for conservation management and potential restoration at our field site.

MATERIALS AND METHODS

STUDY SITE

Our field site was a 125 ha farm in SW England (Norwood Farm, Somerset, UK, 51°18.3’N, 2°19.5’W). Norwood Farm is an organic, mixed lowland farm (artificial chemical fertilisers and pesticides are prohibited) comprising 23 fields of arable (mainly cereal) and grass (short-term leys in arable rotation and permanent pasture) (Fig. S1, see Evans *et al.* 2011 for full site description). Our choice of a single (but typical) study site enabled detailed, within-farm replication across multiple habitats and provided the highly resolved ecological network data necessary for our objectives. We identified and mapped six cultivated (hereafter termed ‘farmed’) and six non-cultivated (hereafter termed ‘non-farmed’) habitat types on the farm using a geographic information system (ArcGIS 9.1, ESRI, California) as follows:

<u>Farmed habitats:</u> 1) Fallow (arable fields that remained uncultivated for a whole year); 2) Ley (rye grass *Lolium* spp. and red clover *Trifolium pratense* mix) that were sown and grown for 2 to 5 years as part of the organic crop rotation); 3) New ley (i.e. clover-rye grass ley which had been newly sown the previous year); 4) Permanent pasture; 5) Lucerne (grown as a crop for silage); and 6) Crops (consisting of spring-sown barley and oats, and winter-sown oats, triticale and wheat).

Non-farmed habitats: 1) Grass margin (i.e. grass strips around cultivated fields, typically 5-10m wide and included within UK agri-environment schemes); 2) Mature hedgerow (average height and width 4.1 m and 3.6 m respectively); 3) New hedgerow (i.e. newly planted hedgerow dominated by young trees <1.5 m high and grass); 4) Rough Ground (i.e. uncultivated areas around farm buildings, machinery storage areas); 5) Standing trees (mature isolated trees in fields); and 6) Woodland.

FIELD SURVEYS

We constructed a highly-resolved network of ecological networks (i.e. species-interaction networks sharing the same plants). This comprised of 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). Our intention was to encompass a wide taxonomic and functional range that included animals regarded as bioindicators and as ecosystem service providers. The networks thus included trophic, mutualistic and parasitic interactions.

We undertook replicated monthly sampling in all habitats (across the entire farm) over two years during 2007 and 2008. The methodological description for vegetation and each animal group is described in the Supporting Information. Unless otherwise stated, we sampled 3-4 randomly located transects per habitat per month (see Table S1 for totals). Species abundance estimates from transects were scaled up to provide a total per habitat, summed across habitats (to give farm-scale monthly totals), summed across months and averaged across the two years to construct the final farm-scale network.

We visualised the networks individually and collectively using Pajek 2.00 (de Nooy *et al.* 2002).

OBJECTIVE 1: Testing the robustness of the network of ecological networks to random habitat loss

We modelled the robustness of each of the animal groups within the network to the sequential removal of habitats. We randomly removed habitats from the networks and plants became extinct when all habitats within which they occurred were deleted. Animal taxa became disconnected (a “secondary extinction”) when all their food species became extinct. If an animal had been observed feeding on a plant in one habitat, then we assumed it could have fed upon it in other habitats, even if the specific animal-plant interaction was not observed in that habitat. In simulating the loss of plants within habitats, we assumed a bottom-up rather than top-down regulation of the animals, as justified by Scherber *et al*. (2010).

We considered two complementary models of robustness: (i) where all taxa are weighted equally (R_S) (Memmott *et al.* 2004) and (ii) the quantitative equivalent (Kaiser-Bunbury *et al.* 2010), where taxa are weighted by their abundance (R_Q, Fig.1A-C), calculating $\bar{R}$ as the average area under the curve of the species/abundance remaining against primary (habitat) extinctions across 10,000 simulations (Burgos *et al.* 2007). Given this approach, our models can be interpreted either as representing the cascading negative effects of habitat loss or the positive cascading effects of habitat restoration. R_S is analogous to assessing effects on species richness, while R_Q is more analogous to assessing effects on species diversity; the quantitative information potentially making it more robust to sampling biases (Banasek-Richter *et al.* 2004). All analyses were carried out using R 2.15.2 (R Development Core Team, 2012).

OBJECTIVE 2. Determining the relative importance of each habitat within the network

We quantified the importance of each habitat to the robustness of each of the 11 animal groups. This was assessed for each habitat *j* from the regression (r_{ij}) of robustness of each animal group *i* (R_S, R_Q) with the order of the habitat in the 10,000 extinction sequences. We calculated the absolute importance of each habitat for each animal group by regressing the robustness from the 10,000 iterations against the order of habitat *j* in the removal sequence: R = C + (β_j x order of habitat *j* in removal sequence), where we interpret β_j as the importance of the habitat *j* (Fig. 1D). Therefore, if habitats have a stronger effect when lost early, the slope of the regression will be steeper, in other words, β_j will be larger. Our rationale is that the 'importance' of a habitat cannot be directly assessed from the number of secondary extinctions caused by its loss (because if lost at the start of the sequence few secondary extinctions will result), but if a habitat is important to the overall integrity of the network, then overall robustness will tend to be lower if it was lost early in the sequence than if it was lost later. To determine the importance of the habitat across all the animal groups, we averaged the importance values (β_j). Thus we consider the importance of habitats relative to each other (rather than ascribing an absolute value of 'importance'). We did this separately for R_S and R_Q and plotted habitat importance against total habitat area (we used the maximum values from Fig. S2). We used these data to rank habitats according to their importance as a new habitat loss scenario for robustness analysis under Objective 4.

OBJECTIVE 3: Examining species similarity and plant spill-over effects between habitats

If the similarity of plants and animals between habitats is low, then our expectation is that the robustness of the animal groups to habitat loss will be low because there are many habitat-specific interactions. Conversely, if there is high similarity, our expectation is that robustness will be high. We estimated similarity across habitats using Chao's Sørensen similarity index for replicated incidence based data (Chao *et al.* 2005) using EstimateS 8.0 (Colwell 2006) (see Supporting Information). We also consider the binary case, assessing similarity with Classic Sørensen indices and present this in Table S2. This data was subsequently used to rank habitats according to their similarity as a new habitat loss scenario for robustness analysis under Objective 4. We then examined the extent to which plant "spill-over" (Brudvig *et al.* 2009) between habitats affected robustness (R_S, R_Q). Our rationale is that because the habitats are spatially close, species that are specialists in one habitat could, by chance, be found at low densities in neighbouring habitats. This would give our networks the appearance of higher robustness than was truly the case. In order to test the sensitivity of our analyses to this effect, we removed these putative spill-over plants from the network. We calculated total plant density for each species in the 12 habitats by dividing the leaf area index (LAI) per plant species by habitat area (Fig. S2). Specifically, LAI per plant species was calculated monthly over two growing seasons (Pocock *et al.* 2010) and we used the overall maximum LAI for each plant species, and habitat area was calculated separately for the two years (which varied slightly due to crop rotations) and we used the maximum annual area of each habitat. We removed plants from the habitats in which their density was <5% of the maximum density for that plant in any habitat (this was an arbitrary threshold, but removed a significant number of plant-habitat associations, see below). We excluded these plants (and their interactions) from the network, repeated the robustness and habitat importance analyses as above and compared results from the two networks.

OBJECTIVE 4: Determining the best- and worst-case habitat loss scenarios

We undertook the random simulations (Objective 1) in order to determine the distribution of robustness. However, because there are 12 factorial (over 479 million) randomly ordered ways of making habitats in our network extinct (hereafter called permutations), the chance of discovering the best and worst habitat extinction permutations for robustness was very low. We therefore used a genetic algorithm (GA) to search across the possible permutations in order to determine the best- and worst- case permutations and recorded both the resulting value of the network's robustness and the order of the habitats in these permutations. Genetic algorithms can be adapted for searches across permutations, and provide an excellent, efficient way of searching for global optima when there are many local optima (Haupt & Haupt, 2004) and they have been successfully used to understand patterns of secondary extinctions in food-web analyses (Allesina & Pascual 2009). We used the package 'GA 1.0' within R 2.15.2 (see Supplementary Information) and ran the genetic algorithm 100 times with randomly-selected starting values in order to be as confident as possible that we identified the global optimum. The value that we were seeking to optimise (i.e. find the minimum or maximum values, depending on whether it was best- or worst-case) was the overall robustness, i.e. the average robustness across the different animal groups (so, in our case, we treated each animal group as equally important, though this can of course be altered; see Pocock, Evans & Memmott, 2010). Having generated information about the distribution of robustness values for our network (i.e. the limits from the GA, and the distribution within these limits from the random permutations), we tested the following *a priori* scenarios (which from 1 to 3 require increasing amounts of information about farm habitats to create the permutation), in determining ‘good’ and ‘bad’ habitat loss scenarios: 1) habitat management – we sequentially removed habitats based on the least-to-most and most-to-least managed/disturbed, which equates to preferentially losing the most natural (i.e. least economically productive) habitats first. We considered this to be a potential (albeit subjective) scenario for agricultural intensification and removed habitats in the following order: Woodland, Standing trees, Mature hedgerow, New hedgerow, Grass margin, Rough ground, Ley pasture, New ley, Permanent pasture, Spring fallow, Lucerne, Crops; 2) habitat importance - we used the habitat importance values derived from the simulations described in Objective 2. Our expectation was that ranking habitats from the highest-to-lowest importance would lead to low robustness, and *vice versa*; 3) habitat similarity – we determined habitat loss scenarios using habitat similarity data from Objective 3. Here, we ranked the habitats according to their similarity based on plant composition. We treated the plant pairwise similarity indices as distances (distance = 1/similarity) and calculated the closeness centrality of each habitat (Freeman 1979), interpreting the least central habitat to be most distinctive in its plant composition. Our expectation was that the most-to-least distinctive habitat loss scenario would result in high robustness, and *vice versa*. In all cases we considered R_S and R_Q separately. In these three cases, we compared the order of habitats in each *a priori* scenario to the order of habitats in the best and worst cases derived from the GA using Spearman's rank correlation, taking the median habitat position in cases where there were multiple solutions from the GA.

RESULTS

The overall farm network comprised 1502 unique interactions (Fig. 2A) between a total of 560 taxa, consisting of plants and the 11 targeted groups of animals (Pocock *et al.* 2012. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.3s36r118).

OBJECTIVE 1: Testing the robustness of the network of ecological networks to random habitat loss

The loss of all semi-natural habitats resulted in a 43% reduction of species within the farm-scale network and a loss of 57% of species interactions (Fig. 2B & D), despite these habitats covering only c. 14% of the total farm area (Fig. S2). Furthermore, when the network was degraded to a point where only crops remained, 66% of species and 87% of interactions were lost (Fig. 2C & D). Despite variation between groups, robustness to the random loss of habitats was generally high ($\overline{R} \rightarrow 1$; Fig. 3) regardless of whether all taxa were weighted equally (R_S) or by their abundance (R_Q).

OBJECTIVE 2. Determining the relative importance of each habitat within the network

When considering the robustness of taxa that are weighted equally (R_S, Fig. 4), we found that the most important habitats were mature hedgerow and rough ground (i.e. uncultivated areas around farm buildings and machinery storage areas). These areas covered just 4.5% of the total farm area (in 2007). The three grassland habitats came out as least important, despite collectively covering over 50% of the total farm area. A reanalysis of the data where taxa were weighted by their abundance ($R_{Q,}$ Fig. 4) support these findings but identified cereal fields as the second most important habitat overall (importance = 0.0027), after rough ground (0.0031) and followed by mature hedgerow (0.0022, Fig. 4). Cereal habitats comprised a large area of land on the farm, and had high plant species richness and abundance (particularly species regarded as weeds). Thus, weighting by species abundance shows cereal fields to be important due to their large area rather than their pro-rata value. Although plant and animal groups varied in their influence in the calculation of importance for a particular habitat (overall importance being the mean importance across groups), we did not find that a single group was consistently influential across habitats (Fig. S3).

OBJECTIVE 3: Examining species similarity and plant spill-over effects between habitats

The 12 habitat networks range in size from 21 to 273 trophic species and their number of interactions ranges from 21 to 753 (Fig. S2). The non-cropped, semi-natural mature hedgerow and rough ground habitats had the highest number of observed species (252 and 273 respectively) and interactions (753 and 688 respectively). Overall, non-cropped semi-natural habitat networks generally had a greater number of species in each animal group than farmed grassland habitat networks (Table S1).

Generally, there was high species similarity between habitats for plants and each of the animal groups studied (Chao's Sørensen similarity index, SI $\rightarrow 1$, Table S2), which, given the assumptions of our approach, explains why the robustness of the groups to the loss of habitats was generally high (R was often > 0.9). With the exception of woodland habitats, the high level of plant similarity suggests that species within habitats are relatively homogenous across the farm as a whole (Table S2). Indeed 33% of plant species in our network occurred in 5 or more of the habitats studied.

Removing spill-over plants from the network at the 5% density threshold resulted in the loss of 87 plant-habitat associations (22% of the overall network). This significantly lowered network robustness for most animal groups (based on random habitat loss scenarios: R_S sign test $x = 9$, $n = 12$, $P = 0.073$; R_Q sign test $x = 12$, $n = 12$, $P < 0.001$, Fig.3). Overall, however, robustness remained high for all groups ($R \rightarrow 1$), and remained so when higher density thresholds were applied (Table S4).

OBJECTIVE 4: Determining the best- and worst-case habitat loss scenarios

We found that the GA efficiently identified a single permutation of habitat extinctions (Table S5) representing the worst-case scenario of minimum robustness (R_S = 0.839, R_Q = 0.705, Fig. 5), and identified numerous unique permutations for qualitative and quantitative robustness, respectively (Table S5), each giving the best-case scenario of maximum robustness (R_S = 0.997, R_Q = 0.995, Fig. 5). Overall, we found that the distribution of robustness values was highly skewed, with many permutations resulting in high robustness, but few resulting in relatively low values of robustness (Fig. 5).

Comparing the results of the three *a priori* habitat loss scenarios with the GA, we found that our subjective ranking based on management intensity was poor at predicting which permutation would have a high and which would have a low robustness (i.e. the correlation of the rank position of habitats in the permutations with the genetic algorithm was very poor, rho < 0; Table 1), highlighting the risks of relying on subjective opinion rather than using evidence-based decision-making. Including information about the similarity of plant composition between habitats did not help to identify the best case permutations, but it was better for identifying the worst case permutations (i.e. the correlation was better: rho = 0.25-0.32; Table 1). Basing habitat loss scenarios on the measures of habitat importance came very close to identifying the best case permuations (rho > 0.9) and better than the other approaches to identifying the worst case permutations (rho > 0.45; Table 1), as identified by the genetic algorithm. Indeed, it was only the worst-case habitat loss scenario based on habitat importance information that was significantly associated with the worst-case permutation from the GA (R_S and R_Q habitat importance (worst): r_s = 0.944, P < 0.001 and r_s = 0.916, P < 0.001 respectively, Table 1). Rough ground, mature hedgerows and cereal fields were consistently identified as significant habitats in the robustness analysis based on the GA and habitat importance information (see Table S5).

DISCUSSION

To our knowledge, this is the first study that has examined the robustness of multiple species-interaction networks to the loss of habitats. The combined theoretical and empirical approach enabled us to identify the most important habitats within the network, and could be further developed for other ecosystems. Simulations suggest that the animal groups in our system are generally robust to habitat loss but that the robustness of some groups varies depending on the order of habitat extinction. This is likely to be because the habitats in our study were generally similar in terms of species composition (despite their outwardly different appearance - a consequence of different dominant plants in each habitat; e.g. oak trees *v.* grass) and had few unique interactions. Below, we address the main limitations of this study and discuss our results, first in the context of our objectives, and then in the wider context of the management and restoration of agro-ecosystems.

Limitations

Our study considered the interactions between shared plants and animals which, due to logistic constraints, are only a subset of the animals and species interactions on this farm. In addition, our models assume that i) with the loss of a habitat-specific food source or host, animals are able to switch to alternate food sources in different habitats and ii) we observed the entire possible host range. We accept that these are simplistic models and do not take account of features such as adaptive rewiring (Valdovinos *et al.* 2010). Despite the large amount of fieldwork which enabled us to construct such a complex, highly resolved network of ecological networks, we are aware of the inherent problems of sampling biases in foodweb analysis (Cohen *et al.* 1993; Goldwasser & Roughgarden 1997; Chacoff *et al.* 2012). We discuss variations in sampling efficiency in the field-based networks elsewhere (Pocock *et al.* 2012). However, we chose relatively simple models with clear assumptions to initiate a novel approach to robustness analysis that incorporates variation in the environment inhabited by species. We therefore interpret ‘robustness’ as a relative index of fragility, rather than an assessment of true extinction rates. The limitations of intensively sampling a single study site are discussed in Evans *et al.* (2011), and so we apply our specific findings to farmland in general with caution.

OBJECTIVE 1: Testing the robustness of the network of ecological networks to random habitat loss

In an earlier study we showed that the robustness of the groups to simulated species extinction varied, with plant-pollinator networks being particularly fragile but that networks linked by shared plants do not strongly co-vary in their robustness (Pocock *et al.* 2012). This suggests that targeted management of one group will not inevitably benefit others. Here, we present a potentially powerful technique that explicitly considers how environmental change affects groups of animals linked by habitat.

Overall, we showed that plant and animal groups at Norwood Farm exhibit high robustness, although there is variation between groups. This was because habitats tended to be similar in terms of species composition (see below) and had few unique interactions, despite considerable variation in management intensity and disturbance between habitats. One explanation for this is that plant species such as thistles (*Cirsium* spp.), buttercups (*Ranunculus* spp.) and clover (*Trifolium* spp.) occur in most of the farm habitats and are disproportionately well linked to many other species on the farm (Pocock *et al.* 2010; Evans *et al.* 2011; Pocock *et al.* 2012). Thus these plants effectively blur the boundaries between habitats when they are considered in the context of the whole farm. Additionally, many of the animal groups operate at spatial scales that incorporate a number of habitats (e.g. flower-visitors, birds and mammals). Using our approach, it would suggest that the loss of a particular habitat has little impact on animals if suitable resources are available elsewhere, although more research is needed to confirm this.

OBJECTIVE 2. Determining the relative importance of each habitat within the network

We developed a new approach for assessing habitat importance in a community context. In our study, two habitats that covered a small proportion of the total farm area (rough ground and mature hedgerow) were disproportionately important. When including information on species abundance, crops become the second most important habitat, partly because they cover a much larger area of the farm. In Europe, the importance of hedgerow habitats for biodiversity is well established (Hinsley & Bellamy 2000; Evans *et al.* 2011), but to our knowledge no study has quantified the importance of rough ground. Rather these habitats tend to be ignored as they are neither farmed nor perceived as natural habitats.

Our approach may have considerable potential for assessing the impacts of habitat modification on species interactions and ecosystem functioning as well as ecological restoration in both natural and managed habitats, the success of which is often regarded as difficult to measure in the field using conventional approaches (Palmer *et al.* 1997).

OBJECTIVE 3: Examining species similarity and plant spill-over effects between habitats

Despite variation in species composition, there was generally high species similarity between habitats and few habitat-specific interactions. Removing spill-over plants from the network did significantly lower the robustness of most groups studies, but nevertheless qualitative and quantitative robustness was still high.

Although crop habitats are important in the farm network, the low management, semi-natural habitats had higher species richness for most groups despite covering a small proportion of the farm area. Indeed, mature hedgerow habitats had the highest number of plant species in the farm network, despite covering <3% of the land area. Moreover these habitats also tended to have highest numbers of species regarded as bioindicators (e.g. butterflies and rodents) and ecosystem services providers (in our case pollinating insects and hymenopteran parasitoid wasps; a natural form of pest control), supporting the findings of previous studies (Macfadyen *et al.* 2009).

OBJECTIVE 4: Determining the best- and worst-case habitat loss scenarios

Our application of a genetic algorithm was an efficient way of determining the best- and worst-case habitat loss permutations (i.e. the limits of the distribution of robustness values), performing better than our subjective habitat-loss scenarios based on management intensity, and could be applied to other ecosystems.

The results of these models showed the importance of the habitat we termed ‘rough ground’ (which is a ruderal habitat with a mix of perennial and annual herbaceous plants and common on most UK farms) to overall robustness. On Norwood Farm, this habitat exists in relatively small patches of field corners, overgrown tracks and next to the farm yard and covers less than 2% of total farm area. We recommend that land managers, conservationists and policy-makers consider its importance.

CONCLUSIONS

Our understanding of the factors determining the robustness of ecological networks to environmental change is still in its infancy, but with growing global pressures on natural resources our need to understand and mitigate the impacts is increasingly important. Incorporating dynamics into ecological network analysis is a research priority (Thompson *et al.* 2012) and this area is undergoing very active research (Bastolla *et al.* 2009; James *et al.* 2012). However, there is still an important role for structure-based network analyses because they can reveal important changes in community structure and ecosystem functions as a result of environmental change (Tylianakis *et al.* 2007). Furthermore, recent advances have enabled the incorporation of species abundance in robustness models (Kaiser-Bunbury *et al.* 2010), likely changes in trophic interactions (‘rewiring’) following species loss (Staniczenko *et al.* 2010) as well as cascading effects across multiple groups of animals (Pocock *et al.* 2012). Here we investigated the robustness of a network to habitat loss, one of the most widespread threats to biodiversity. By integrating the role of the environment more generally into ecological network studies, this is likely to offer new perspectives on the structure and dynamics of complexity in nature and thereby provide ways to predict and mitigate the detrimental impacts of environmental change.

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TABLE 1. Average qualitative (R_S) and quantitative (R_Q) network robustness for the plant and animal groups based on a) random habitat loss; b) ranking habitat on management intensity; C) ranking habitat using plant similarity indices; c) ranking habitat using measures of habitat importance; and d) genetic algorithm permutations (*n* = number of solutions, see Material and Methods). Spearman rank correlation coefficients based on relationships between robustness measures from the genetic algorithms best- and worst-case permutations and those from the habitat management, similarity and importance analyses.

		Random habitat loss					**Management Intensity**		**Habitat Similarity**		**Habitat Importance**		**Genetic Algorithm**	
		Min	**LQR**	**Median**	**UQR**	**Max**	**Worst**	**Best**	**Worst**	**Best**	**Worst**	**Best**	**Worst**	**Best**
R_S	R	0.843	0.960	0.974	0.987	0.997	0.975	0.983	0.903	0.980	0.846	0.995	0.839	0.997
	rho	-	-	-	-	-	-0.146	0.091	0.252	0.036	0.944	0.527	-	-
	P	-	-	-	-	-	0.651	0.779	0.430	0.911	0.000	0.079	-	-
	n	-	-	-	-	-	-	-	-	-	-	-	1	958
R_Q	R	0.712	0.924	0.963	0.977	0.995	0.978	0.944	0.869	0.974	0.727	0.993	0.705	0.995
	rho	-	-	-	-	-	-0.378	0.035	0.322	0.234	0.916	0.447	-	-
	P	-	-	-	-	-	0.227	0.913	0.308	0.464	0.000	0.145	-	-
	n	-	-	-	-	-			-	-	-	-	1	434

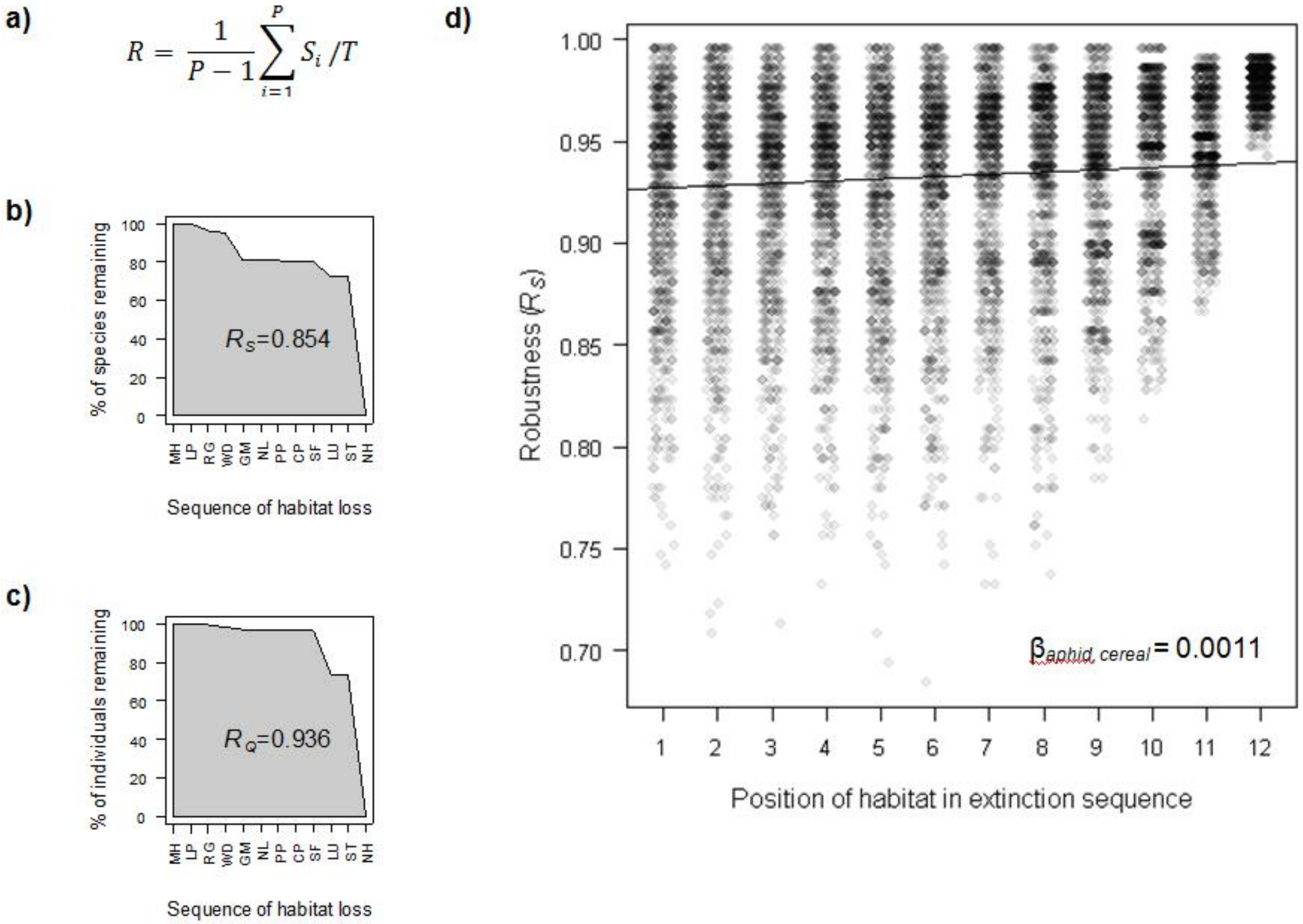

FIGURE 1. Calculating the robustness and habitat importance for plant and animal groups at Norwood Farm. Here, we use an example for seed-feeding invertebrates taken from 10,000 random habitat loss simulations. We calculate robustness R (either R_S or R_Q) where P is the number of primary extinctions (in our case the 12 habitats), S is the number of dependents remaining after the cumulative extinctions of $P_{[1]}$ to $P_{[i]}$ and T is the total number of dependents. For S and T, each species is weighted equally (for Rs) or weighted by their abundance (for R_Q). The robustness of seed-feeding invertebrates to one random sequence of habitat loss is the area under the curve for (b) the qualitative case (species remaining) and (c) the quantitative case (individuals remaining). Habitats are coded as follows: CP, Crops; SF, Spring fallow; GM, Grass margin; LP, Ley pasture; LU, Lucerne; MH, Mature hedgerow; NH, New hedgerow; NL, New ley; PP, Permanent pasture; RG, Rough ground; WD, Woodland; ST, Standing trees. The importance of each habitat for animal groups (d) was calculated by regressing the robustness from the 10,000 iterations against the order of habitat j in the removal sequence: R = C + (β_j x order of habitat j in removal sequence), where we interpret β_j , averaged across animal groups, as the importance of the habitat j.

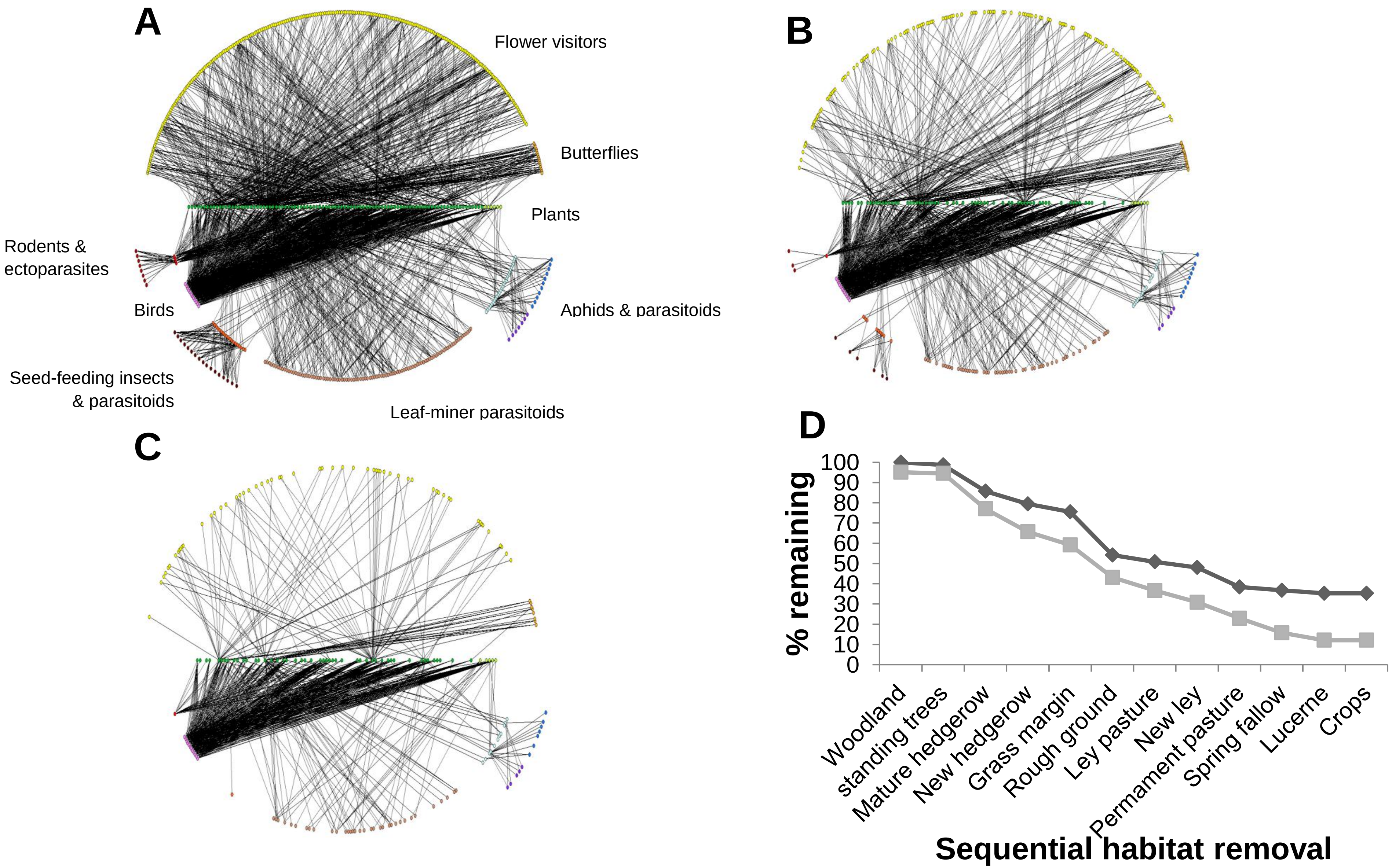
A
Flower visitors
Butterflies
Plants
Rodents &
ectoparasites
Birds
Aphids & parasitoids
Seed-feeding insects
& parasitoids
Leaf-miner parasitoids
B
C
D
% remaining
100
90
80
70
60
50
40
30
20
10
0
Woodland
standing trees
Mature hedgerow
New hedgerow
Grass margin
Rough ground
Ley pasture
New ley
Permament pasture
Spring fallow
Lucerne
Crops
Sequential habitat removal

FIGURE 2. The result of habitat loss on species and species interactions on the Norwood Farm network of networks. The complete network (A) is degraded by sequentially removing the species and interactions that occur in each of the farm habitats. In this case, habitats are removed in order of least management until all semi-natural habitats have gone (B) and when only crops remain (C). Regions with very dense links primarily represent the interactions of generalist seed-feeding birds taken from the literature. In the graph (D) diamonds and squares represent the percentage of species and interactions respectively that remain in the network after habitat loss from least to most managed.

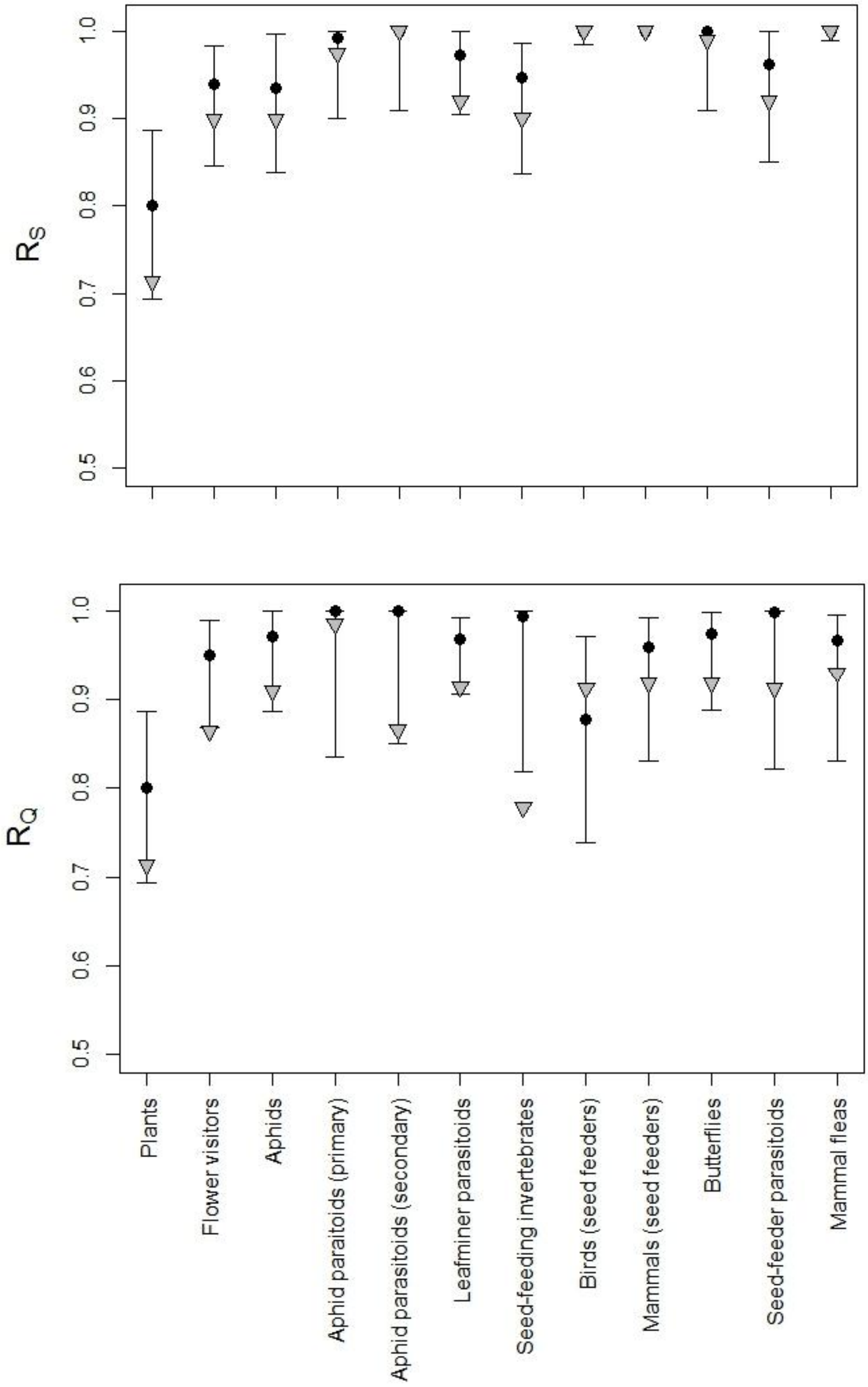

FIGURE 3. The qualitative (R_S) and quantitative (R_Q) robustness of plant and animal groups at Norwood Farm, England to simulated random habitat loss based on a) the complete network of ecological networks (● median with 95% error bars) and b) the network after 'spill-over' plants and their interactions were excluded (▼ median) based on a 5% density threshold (see Methods and Materials).

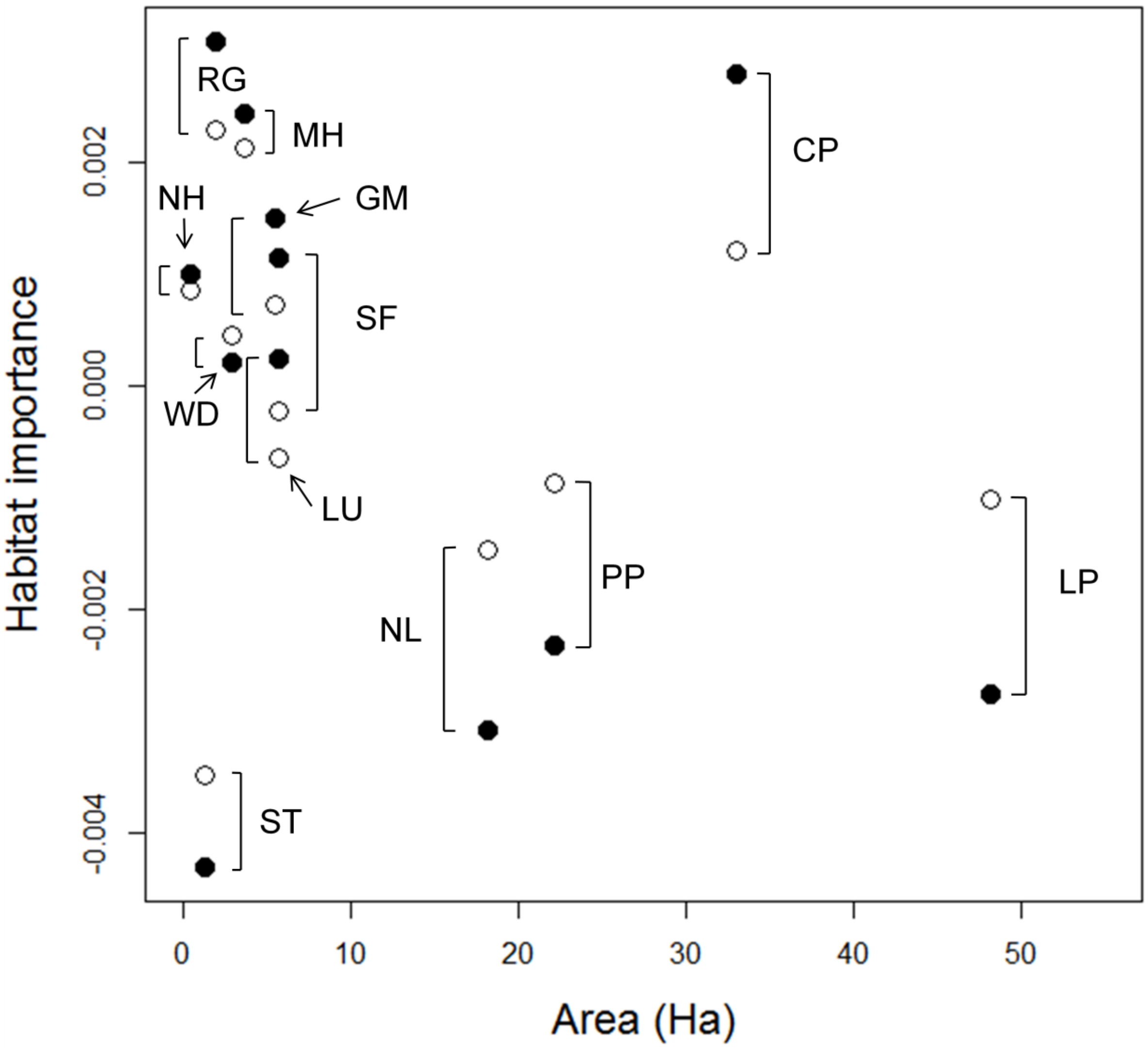

FIGURE 4. The importance of habitats in the Norwood Farm network of networks, in relation to habitat area, using qualitative (○) and quantitative (●) data. Habitat codes are given in Fig. 1. Habitats covering small areas tended to be more important in the networks, although cereal field weeds increased the importance of crops.

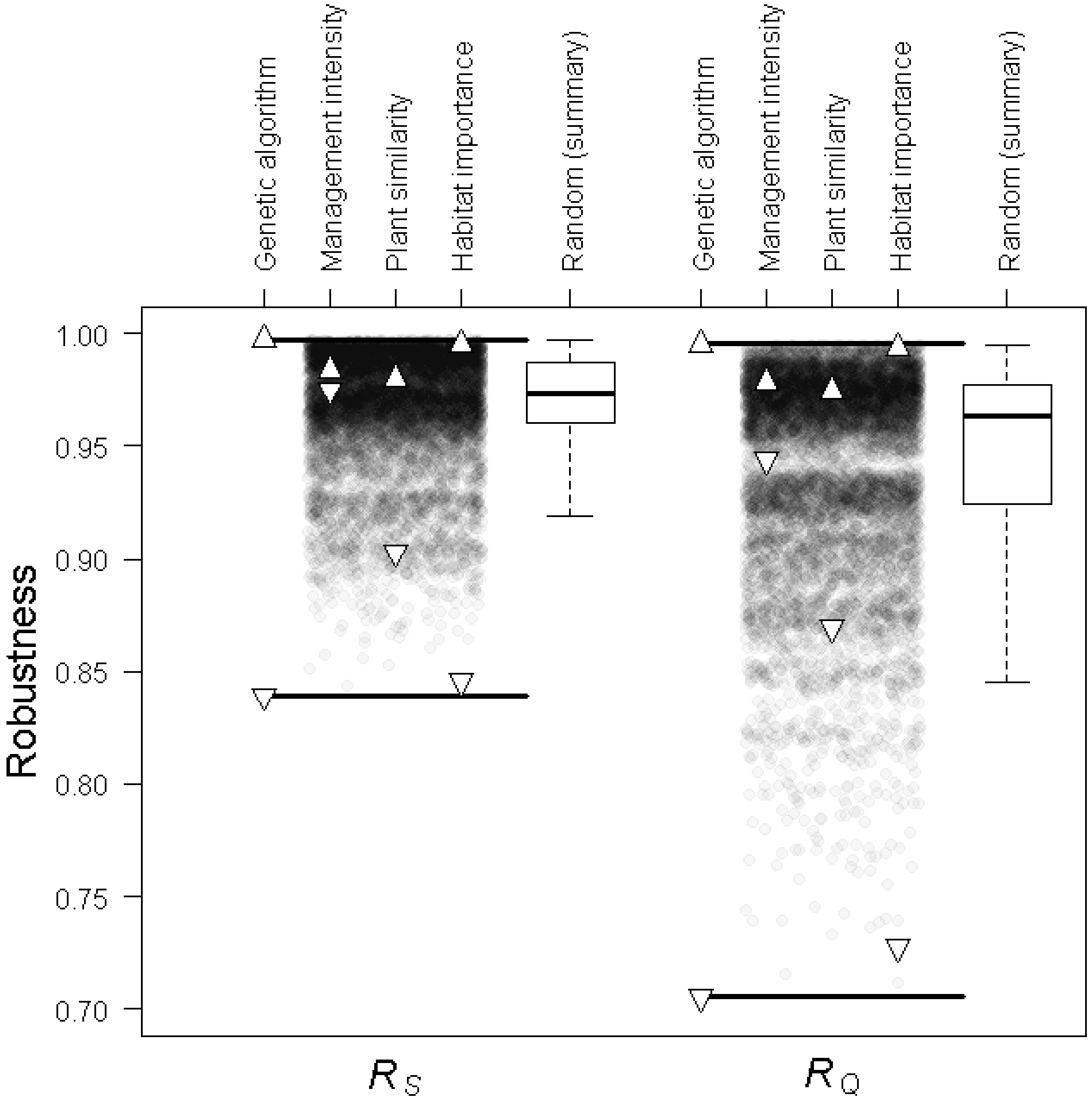

FIGURE 5. The robustness ($\bar{R}$) of the Norwood Farm network to habitat loss. Here is shown the 10,000 random permutations (shown with dots, and for ease of interpretation summarised in the boxplot), with the maximum and minimum from the genetic algorithm (thick horizontal bars) and the expected best and worst case permutations (triangles pointing up and down, respectively), based on management intensity, similarity of the plant composition and habitat importance from the whole network analysis. We show results where all taxa are weighted equally (R_S) and the quantitative equivalent, where taxa are weighted by their abundance (R_Q).

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