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Plant species roles in pollination networks: an experimental approach

Pereira Maia, K., Vaughan, I.P. & Memmott, J.

Abstract

Pollination is an important ecosystem service threatened by current pollinator declines, making flower planting schemes an important strategy to recover pollination function. However, ecologists rarely test the attractiveness of chosen plants to pollinators in the field. Here, we experimentally test whether plant species roles in pollination networks can be used to identify species with the most potential to recover plant-pollinator communities. Using published pollination networks, we calculated each plant's centrality and chose five central and five peripheral plant species for introduction into replicate experimental plots. Flower visitation by pollinators was recorded in each plot and we tested the impact of introduced central and peripheral plant species on the pollinator and resident plant communities and on network structure. We found that the introduction of central plant species attracted a higher richness and abundance of pollinators than the introduction of peripheral species, and that the introduced central plant species occupied the most important network roles. The high attractiveness of central species to pollinators, however, did not negatively affect visitation to resident plant species by pollinators. We also found that the introduction of central plant species did not affect network structure, while networks with introduced peripheral species had lower centralisation and interaction evenness than networks with introduced central species. To our knowledge, this is the first time species network roles have been tested in a field experiment. Given that most restoration projects start at the plant community, being able to identify the plants with the highest potential to restore community structure and functioning should be a key goal for ecological restoration.

Key-words: pollination networks, species roles, centrality, peripheral, field experiment, network structure

Introduction

Pollination is an important ecosystem service, provided mainly by insect pollinators. It is estimated that 75% of crops species (Klein et al. 2003) and 87.5% of flowering plant species in general (Ollerton et al. 2011) depend on animal pollination, and in recent years the demand for crop pollination by insects has tripled (Aizen and Harder 2009). However, current pollinator declines caused mainly by habitat loss (Potts et al. 2010), farming intensification (Sanchez-Bayo and Goka 2014) and insect diseases (Goulson et al. 2015) could disrupt pollination services. To ensure the integrity of natural ecosystems (Ashman et al. 2004, Aguilar et al. 2006) and the productivity of insect-dependent crops (Klein et al. 2007), healthy pollinator populations need to be supported.

Decreasing floral resources due to habitat loss and degradation is a key contributor to current pollinator declines (Carvell et al. 2006, Kleijn and Raemakers 2008, Roulston and Goodell 2011). Even when non-lethal, the lack of good feeding habitats can make insects more prone to more harmful stressors such as diseases and pesticides (Alaux et al. 2010, Goulson et al. 2015). Therefore, flower planting schemes are an important strategy to recover pollination function in both agricultural (Pywell et al. 2005) and urban areas (Blackmore and Goulson 2014). Since diverse pollinator communities increase the quality and stability of pollination services (Hoehn et al. 2008, Winfree and Kremen 2009, Albrecht et al. 2012, Orford et al. 2016), plant species which are able to attract and support a high diversity and abundance of pollinators need to be identified (Dixon 2009).

Currently, species lists for seed mixes and planting plans are put together using expert knowledge rather than rigorous field trials on how a community of plants interacts with a community of pollinators. An alternative approach is to use ecological networks to identify species with structural and functional importance in pollination systems (Martín-González et al. 2010, Coux et al. 2016). Pollination networks are formed by a core of well-connected

generalist plant and insect species with which many specialist species interact (Bascompte et al. 2003). This structure is thought to promote network robustness and to increase the resilience of pollination networks due to high levels of redundancy (Memmott et al. 2004, Burgos et al. 2007, Bastolla et al. 2009, Song et al. 2017). Given that species forming the network core are structurally and functionally important in pollination systems (Vázquez and Aizen 2004, Coux et al. 2016), ecological restoration could focus on these plant species. Equally, species that are peripheral, falling outside the core, may be a poor choice for restoration as they could provide food for a small proportion of pollinator species. Our aim in this paper is to explore how plant species with contrasting network roles in natural plant-pollinator communities perform when introduced into existing plant communities. As the aim of ecological restoration is to recover community structure and function, the use of ecological networks could prove to be an insightful approach since networks characterise the structure of species interactions at the community level.

Core plant species usually have high levels of centrality. Centrality metrics describe the contribution of individual species to network structure. Species with high centrality interact with a high proportion of pollinator species and, therefore, have a high chance of being at short distances (measured in number of interactions) to most species in the network and located along the shortest paths connecting other species pairs (Martín-González et al. 2010). Central plant species in pollination networks might, therefore, provide a shortcut when the ultimate aim of restoring plant communities is to restore pollinator communities. Given that plant species share and compete for pollinators, the effect of introducing new plants to recover pollination function could also affect the resident plant species. Introducing plant species with high centrality (potentially species presenting attractive traits), for instance, might benefit resident plant species due to pollinator spill-over (Morandin and Kremen 2013, Blaauw et al. 2014). Individuals from a non-rewarding orchid species, for instance, had

higher pollination success when in proximity to highly rewarding species (Johnson et al. 2003). Alternatively, the attractiveness of introduced central plant species to pollinators could result in lower visitation to resident plant species. For instance, visitation to resident plant species might be positively affected by higher richness and diversity of neighbouring flowers, but negatively affected by the generalisation level of neighbouring plants (Lázaro et al. 2009). If we are to fully understand the impact of using central plant species to recover pollination function, in addition to studying their impact on pollinators, we also need to assess their effect on resident plant species and on emerging network structure, as this affects community function and persistence (Tylianakis et al. 2010).

In our study we use a field experiment to test whether species roles in pollination networks can be used to identify plant species with the most potential to recover plant-pollinator communities. Our overall aim is to provide a conceptual framework for choosing the most effective plant species for the restoration of plant-pollinator communities with the use of ecological networks. Specifically, we ask three questions: 1) Do central plant species attract a higher diversity of pollinators than peripheral species? Since high centrality is a measure of structural importance, we expect central plant species to attract higher pollinator diversity than peripheral species; 2) After introduction, which network roles are occupied by the introduced species, and how does species introduction affect visitation to resident plant species? We expect central species, but not peripheral species, to occupy the most important network roles by monopolising interactions with pollinators; consequently, we also expect resident plant species to be less visited in networks with introduced central species when compared to networks with introduced peripheral species; 3) Does the introduction of peripheral and central species promote a different network structure? We expect interactions to be concentrated by few species in networks with introduced central species, making these

networks more centralised and with lower levels of interaction evenness than networks with introduced peripheral species.

Material and Methods

Our study has three components. Focusing on 17 published pollination networks collected in English meadows, we first quantified the centrality of each plant species and selected five central and five peripheral plant species across all networks. We then introduced these 10 species into experimental plots where we collected visitation data for both introduced and resident plant species. Finally, we constructed pollination networks for the experimental plots with the visitation data, to test the impact of the introduced plants on pollinators, resident plants and network structure. While based on data from 17 networks, our experiment was performed at a relatively small scale. Nevertheless, our study provides the beginnings of a conceptual framework for exploring the impact of species-level network metrics in the field, highlighting their potential for use in the ecological restoration of species interactions.

Identifying central and peripheral plant species in plant-pollinator networks

To identify central and peripheral plant species in plant-pollinator communities, we investigated the roles of plant species in 17 published plant-pollinator networks (Supplementary material Appendix 1, Table A1). All these networks were collected in English meadows, most of them (15 out of 17) in southwest England, these being networks from similar systems to our intended experimental plots. We removed grass species from the analysis since they are wind pollinated (Supplementary material Appendix 1, Table A1), even if pollinators do feed on their pollen (Orford et al. 2016).

We used three centrality metrics which are commonly studied in combination given their complementary properties (Martín-González et al. 2010, Emer et al. 2016). Each metric describes the importance of plant species at different scales within the network: normalised degree (ND) is a measure of generalisation, while closeness and betweenness centrality (CC and BC) describe how species are connected to other species in the network through indirect pathways. In common, all indices capture some aspect of pollination niche overlap between plants and, therefore, their potential to attract pollinators, which could benefit resident species. The three metrics are binary, *i.e.* not accounting for the frequency of interaction between species. Central species may present attractive traits for pollinators, for instance by providing high nectar content (Cusser and Goodell 2014). Alternatively, high centrality may be due to sampling bias, that is when abundant species are more frequently sampled than rarer species (Vázquez et al. 2009, Gibson et al. 2011). To control for the latter scenario and to focus on species whose centrality measures truly reflect attractiveness to pollinators, we compared the observed centrality of each plant species in each network with a null expectation based on their relative abundance (Supplementary material Appendix 1, *Identifying central and peripheral plant species*). Our final centrality measure reflects plant species attractiveness to pollinators, being correlated with the abundance and richness of insects visiting plant species (Supplementary material Appendix 1, Fig. A1).

After calculating species centrality, and controlling for species abundance, we ranked the 60 plant species present in the 17 networks from the species with the highest to the lowest centrality across networks (Supplementary material Appendix 1, *Identifying central and peripheral plant species*, Table A2). Finally, we selected five plant species from the top 20 ranked species (central species) and five from the bottom 20 (peripheral species) as focal species whose community role would be tested in a field experiment (Fig. 1, Supplementary material Appendix 1, Table A2). Their flowering period and availability from wildflower

suppliers were the main criteria used for selection, with preference for species flowering in July and August to ensure co-flowering for the experiment. These criteria resulted in our central species being *Achillea millefolium*, *Centaurea nigra*, *Eupatorium cannabinum*, *Knautia arvensis* and *Leontodon hispidus* and our peripheral species being *Agrimonia eupatoria*, *Centaurium erythraea*, *Lotus corniculatus*, *Lychnis flos-cuculi* and *Prunella vulgaris* (see Supplementary material Appendix 1, Table A2 for species' family information).

We did not control for taxonomy in our selection of plant species, and four central species belong to the Asteraceae family, while none of the peripheral species do. The preponderance of Asteraceae species amongst the central group reflects a natural bias, since Asteraceae species in our dataset frequently presented high values of centrality (*i.e.* were among the top ranked species, Supplementary material Appendix 1, Table A2). With a simple randomisation test (plant Family randomised in Supplementary material Appendix 1, Table A2), we found Asteraceae species to rank higher than expected by chance ($p<0.001$).

Experimental design and sampling procedure

Our experimental plots were in two adjacent areas of grassland in Bristol, UK (51°48'N, 2°62'W) separated by large buildings, and the two plots (Plot A and Plot B) were c. 370 m apart (Supplementary material Appendix 1, Fig. A2). Resident plant species had a uniform distribution (*i.e.* spatial configuration) within plots, but the set of resident species was different between the two plots (Supplementary material Appendix 1, Table A3). Each of the two plots had 30 subplots, 2m x 2m in size and 1m apart from each other, these providing the experimental replicates: 10 of these were planted with central species, 10 with peripheral species and 10 were left as controls. To avoid the effect of particularly attractive or unattractive species confounding our results (as we would not be able to separate a treatment effect from a species effect) we introduced three central or peripheral species in each subplot,

this providing 10 unique trios per treatment in both plots (Fig. 1a). In October 2016, we planted the 10 trios of both treatments (Fig. 1b), reducing the immediate competition from the resident plants by using weed-supressing mats (40 cm x 40 cm) around each experimental plant to allow them to establish. Weed-supressing mats were also placed in control subplots.

From May to September 2017 we sampled and collected pollinators 22 times in Plot A and 20 times in Plot B using timed observations, such that each subplot was observed for 15 minutes per sampling occasion. Sampling completeness, measured as observed pollinator richness divided by estimated richness (Chao estimate), was similar among subplots of different treatments (Control: mean = 0.41, sd = 0.21, Peripheral: mean = 0.43, sd = 0.15, Central: mean = 0.41, sd = 0.18**,** p = 0.94). Weekly, we counted the flower units of all flowering species (resident and introduced) in all subplots. A flower unit was defined as one or more flowers that insects could access without flying (Carvalheiro et al. 2008, Baude et al. 2016), *e.g.* for Asteraceae a flower unit is a whole inflorescence while in Rosaceae it is one flower (Supplementary material Appendix 1, Table A4). Therefore, even if a floral unit represents a different number of flowers for different plant species, it is defined from the insect's perspective which, in the context of this study, is a more meaningful measure of floral abundance (Carvalheiro et al. 2008). At the end of the season, all insects were identified by taxonomists (see acknowledgements). Most insect species (80.1%) and individuals (91.4%) were identified to the species level. The proportion of species and individuals which were not identified to the species level is consistent across subplots of different treatments (species: $F_{(2,57)} = 0.58$, p = 0.56, individuals: $F_{(2,57)} = 1.5$, p = 0.23).

Calculating network metrics

We constructed one quantitative pollination network per subplot, such that the interactions sampled in control, peripheral and central subplots resulted in 20 control, 20

peripheral and 20 central networks, respectively, 10 of each treatment from each experimental plot (Fig. 2 and Supplementary material Appendix 1, Fig. A3). All species-level and network-level metrics described below were calculated with *bipartite* and *sna* R packages (Dormann et al. 2009, Dormann 2011, Butts 2016).

To test whether the species network roles measured from the published networks hold under experimental conditions (Question 2), *i.e.* whether central species occupy the most important network roles after introduction, we used two species-level metrics: normalised degree, previously used to define central and peripheral species, and partner diversity, a quantitative metric that accounts for the frequency of interactions between species. We chose these two metrics as they have a clear meaning even in small networks. Partner diversity is the Shannon diversity index calculated for the interactions of each species, high values indicating even spread of interactions across partners and low values indicating interactions being dominated by few partner species. Since we expect central species, but not peripheral species, to monopolise pollinators, we expect central species to have higher normalised degree and partner diversity than resident plant species in central networks, while peripheral species will have similar network roles to resident species in peripheral networks.

To investigate how the introduction of central and peripheral plant species affected the structure of our experimental networks (Question 3), we used two network-level metrics: closeness centralisation and interaction evenness. The first metric is binary, while the second is quantitative. Closeness centralisation is a network-level metric based on the species-level metric closeness centrality, and it measures the difference between the centrality of each species to the maximum centrality value of the network (Freeman 1979, Butts 2016). We calculated closeness centralisation straight from the bipartite network (instead of using the unipartite projection), in order to obtain meaningful distances in these smaller networks. Interaction evenness is similar to partner diversity but calculated at the network-level,

measuring the equitability of network interactions and describing whether the frequency of interactions is evenly distributed or if a handful of interactions dominate the network (Tylianakis et al. 2007). Since we expect central species to occupy the most important network roles when introduced by monopolising interactions with pollinators, we expect the central networks to have higher centralisation, but lower interaction evenness than peripheral networks.

Question 1: Do central plant species attract a higher diversity of pollinators than peripheral species?

To test whether subplots with introduced central plant species attract a higher abundance and richness of pollinators than subplots with introduced peripheral species, we used general linear mixed models (GLMM) with a Poisson distribution. To account for the variation in *exposure*, *i.e.* flower abundance, between subplots (Supplementary material Appendix 1, Fig. A4, Table A5), we included floral abundance per subplot as an offset variable (Reitan and Nielsen 2016). Offset variables allow count data to be analysed as rates, without actually transforming the count data into a rate to avoid information loss (Reitan and Neilsen 2016). We use flower abundance as a measure of exposure since, when assuming neutral encounters between plant and pollinator species, an increase in flower abundance increases the chance of encounters. Fixed effects were treatment, plant richness in the subplot since plant richness, in addition to abundance, could affect pollinator richness and abundance (Potts et al. 2003, Orford et al. 2016), and experimental plot. Each observation corresponded to data collected from each subplot during each sampling event. Therefore, to account for the repeated measures of each subplot, we included subplot as a random effect. The significance of fixed effects was assessed with likelihood ratio tests as these represent a good trade-off

between reliability and simplicity. The effect of treatment was further investigated with Tukey tests using the *emmeans* R package (Lenth 2018).

Question 2: After introduction, which network roles are occupied by the introduced species, and how does species introduction affect visitation to resident plant species?

To investigate the network roles played by introduced species in our experimental networks, we compared the network roles (normalised degree and partner diversity) of introduced species versus resident in peripheral and central networks. We expect central, but not peripheral species, to occupy the most important roles in their networks when compared to resident species in those networks. For this analysis, species-level metrics were used in two separate linear mixed models (LMM) as response variables. The interaction between species status (resident versus introduced) and treatment, plus species abundance and experimental plot were included as fixed effects. Random effect structure was selected with Akaike Information Criteria (AIC, Zuur et al. 2009) between: (i) no random effect, (ii) species identity, (iii) subplot, and (iv) species identity and subplot.

To test the effect of species introduction on visitation to resident species, we compared the abundance and richness of insects visiting resident species among control, peripheral and central networks. We expect decreasing visitation to resident species from control to peripheral to central networks, due to increased competition after species introduction and attractiveness of central species. Abundance and richness of flower visitors were used in two separate GLMM with a Poisson distribution. As each observation corresponded to one resident species, at the subplot level, to account for the variation in floral abundance across resident species, and within species across subplots, we included the floral abundance of each resident species in each subplot as an offset variable (Reitan and Nielsen 2016). We included treatment and experimental plot as fixed effects. Random effect structure

was selected with AIC between: (i) no random effect, (ii) species identity, (iii) subplot, and (iv) species identity and subplot. Since resident species might respond differently to species introduction depending on their own centralities, we performed the same analysis including only the five resident species with a peripheral status (Supplementary material Appendix 1, Table A2, Table A3). The significance of fixed effects was assessed with likelihood ratio tests.

Question 3: Does the introduction of peripheral and central species promote a different network structure?

To investigate the effect of species introduction on network structure we performed separate linear models (LM) for each network-level metric (closeness centralisation and interaction evenness). Four control networks were excluded from the analysis due to their small size – either networks with less than five species (plants and pollinators), and/or with only one species in one of the sets (plants or pollinators, Supplementary material Appendix 1, Table A6). Since network metrics are dependent on the number of species in the network, and number of species was likely to vary across treatments, the metric values were normalized. Interaction evenness is normalised when calculated in *bipartite* R package (Dormann et al. 2009) and closeness centralisation was normalised by comparing the observed value of each network with the theoretical maximum centralisation for that network (Butts 2016). After normalisation, both network-level metrics were not correlated with network size (Supplementary material Appendix 1, Fig. A5). Models for each network-level metric had treatment and experimental plot as explanatory variables.

Results

In total 1876 insects and 171 insect species were collected from the two plots: 910 insects and 129 species in Plot A, and 966 insects and 108 species in Plot B (Supplementary material Appendix 1, Table A7). In addition to the 10 species of plant which were added to the plots, a further 17 plant species were found growing naturally in the plots, 8 in Plot A and 14 in Plot B (Supplementary material Appendix 1, Table A3).

Question 1: Do central plant species attract a higher diversity of pollinators than peripheral species?

In both plots, the observed abundance and richness of pollinators increased from control to peripheral to central subplots (Fig. 3). Our models show that treatment had a significant effect on both pollinator abundance ($\chi^2(_2) = 50.8$, $p < 0.001$) and richness ($\chi^2(_2) = 48.12$, $p < 0.001$). As the offset variable included in the models accounts for differences in subplot floral abundance between treatments, our models show that peripheral subplots attracted significantly fewer insect individuals ($p = 0.01$) and species ($p = 0.004$) than control subplots, while central subplots attracted significantly more insect individuals and species than both peripheral and control subplots ($p<0.001$ for all comparisons, Table 1). Plant richness had a negative effect on insect abundance ($\chi^2(_1) = 25.10$, $p < 0.001$) and richness ($\chi^2(_1) = 23.21$, $p < 0.001$). Experimental plot was removed from both models (abundance: $p = 0.15$, richness: $p = 0.18$).

Question 2: After introduction, which network roles are occupied by the introduced species, and how does species introduction affect visitation to resident plant species?

Experimental networks had on average 4.12 flowering plant species (min=1, max=9, mean plant species in control=2.6, peripheral=5.1 and central=4.65 networks) and 16.8 insect species (min=2, max=37, mean insect species in control=9.45, peripheral=16.35 and

central=24.65 networks, Supplementary material Appendix 1, Table A6). As expected, introduced central species had significantly higher values of normalised degree (p=0.007) and partner diversity (p=0.005) than resident species in central networks, while introduced peripheral species had similar values for both metrics to resident species in peripheral networks (normalised degree: p=0.99, partner diversity: p=0.99, Fig. 4a-b). Floral abundance had a positive effect on both species-level metrics (normalised degree: $\chi^2(_1) = 13.37$, $p < 0.001$, partner diversity: $\chi^2(_1) = 26.32$, $p < 0.001$), whilst both metrics were on average lower in Plot B than in Plot A (normalised degree: $\chi^2(_1) = 5.93$, $p = 0.01$, partner diversity: $\chi^2(_1) = 5.68$, $p = 0.02$). Only species identity was included in the selected random structure for normalised degree, while species identity and subplot were included for partner diversity.

No effect of treatment was detected on visitation to resident species, as resident species were visited by similar numbers of insect individuals (p=0.2) and species (p=0.16) in all treatments (Fig. 4c-d). Therefore, contrary to our expectations, introduced central species did not appear to monopolise interactions at the expense of resident plant species. Experimental plot, on the other hand, had a significant effect on visitation to resident plant species, as resident species were visited by fewer insect individuals ($\chi^2(_1) = 18.92$, $p < 0.001$) and species ($\chi^2(_1) = 11.05$, $p < 0.001$) in Plot B. For both models, species identity and subplot were included in the selected random structure. Finally, performing the same analysis but only including the five resident species with a peripheral status, produced qualitatively similar results as no effect of treatment on visitation to these species was detected (Supplementary material Appendix 1, Fig. A6).

Question 3: Does the introduction of peripheral and central species promote a different network structure?

At the network level, we expected the introduction of central species to increase network centralisation, but to decrease interaction evenness. Centralisation was lower in peripheral than in central networks, but central networks were not more centralised than control networks ($F_{(2,53)} = 7.85$, $p = 0.001$, Fig. 5a). But contrary to our expectation, interaction evenness was higher in central than in peripheral networks but no different to control networks ($F_{(2,53)} = 3.86$, $p = 0.03$, Fig. 5c). Experimental plot was removed from both models (centralisation: $p = 0.27$, interaction evenness: $p = 0.84$).

Discussion

To our knowledge, this is the first field test of species network roles, specifically of whether centrality metrics capture the importance of plant species for the pollinator community. As predicted, we found that species' network roles were conserved when introduced into new communities: introduced central plant species attracted a higher richness and abundance of pollinators than peripheral species, and occupied the most important network roles after introduction. The high attractiveness of central species to pollinators, however, did not affect either visitation to resident plant species or overall network structure. The introduction of peripheral species decreased network centralisation and resulted in networks with lower interaction evenness. In what follows we first address the limitations of our study, and then consider our results in the context of previous findings and discuss the potential use of ecological networks in restoration programmes.

Limitations

There are two main limitations in our study. First, as the spatial scale of our study is small, we observed behavioural rather than populational responses, and spill-over of pollinators between subplots of different treatments might have occurred. If spill-over did

occur from central to peripheral and control subplots, then the higher pollinator diversity found in central subplots is a conservative result; but the small difference in visitation to resident species and network structure between treatments should be interpreted with caution. Alternatively, if central plants do attract pollinators at the expense of resident species, some spill-over might have occurred from control to central plots. If that is the case, the attractiveness of central species to pollinators could have left no mark on visitation to resident species in central plots. Second, our experiment is a short term one, run for one field season only. While there is no obvious reason why running the experiment in spring or in the autumn would affect our results, it would be good to have a greater degree of spatial and temporal variation, the former perhaps using plant communities from very different habitats and the latter including data from different years.

Plant species roles in pollination networks

We found that introduced central species attracted a significantly higher abundance and richness of pollinators than introduced peripheral species. We emphasise that our centrality measure captures more than plant species abundance, as abundance was accounted for during centrality calculations. Therefore, for our system, plant species network roles in natural communities accurately predicted their importance for pollinators in our experimental arrays, and likely in other plantings. The high correlation between plant species centrality and attractiveness to pollinators (richness and abundance of visitors) can be useful for ecological restoration. By choosing plant species visited by a diversity of partners, one will be indirectly selecting species that increase pollination niche overlap among plants and connect potentially isolated parts of the network (Martín González et al. 2010, Emer et al. 2016).

We did not control for variation in species morphology or nectar content between treatments, even if these attributes are known to mediate plant-pollinator interactions (Stang

et al. 2006, Santamaría and Rodríguez-Gironés 2007, Junker et al. 2013, Lihoreau et al. 2016). In fact, introduced central and peripheral species presented a different set of functional traits, with central species having a more constrained set of traits than peripheral species (Supplementary material Appendix 1, Figure A7), probably stemming from the high prevalence of Asteraceae among central species. Flowers with more accessible nectar tubes could be visited by a wider range of insect species (Stang et al. 2006, Campbell et al. 2012), and plants with higher nectar content could potentially receive more visits than species with less nectar (Lihoreau et al. 2016). Together with high abundance (Fort et al. 2016), traits such as generalist flower morphologies and high nectar concentration are likely associated to central roles of plant species in pollination networks. Evaluating which morphological traits are associated with plant species centrality, while not the focus of this study, would be an interesting future study and an important contribution to flower planting schemes.

Asteraceae flowers generally possess the attractive traits which are expected to be associated with high visitation rates, such as open flowers with high nectar content (Baude et al. 2016). However, their nectar and pollen may not be as readily available or beneficial to all pollinators (Sedivy et al. 2011, van Rijn and Wäckers 2016, McAulay and Forrest 2018). For instance, Asteraceae pollen may not be optimal for generalist bees, due to its low nutritional content and/or toxicity (Nicolson and Human 2013, Eckhardt et al. 2014). In fact, generalist bees benefit from a mixed pollen diet (McAulay and Forrest 2018). Therefore, in order to favour multiple pollinator groups, flower planting schemes should concomitantly assess plant species attractivity and palatability.

We expected central, but not peripheral, species to occupy the most important roles in their networks, by outcompeting resident species and concentrating most interactions for themselves (Bjerknes et al. 2007, Morales and Traveset 2009). Indeed, we found that plant species' original roles did hold under experimental conditions: introduced central species

occupied the most important network roles in experimental conditions whereas peripheral species continued to act as peripheral. However, the introduction of central and peripheral species did not affect pollinator visitation to resident species: resident species interacted with similar numbers of pollinator individuals and species regardless of the type of species added to the plots. The potential for a flowering species to influence its neighbours depends on its reward availability and accessibility (Carvalheiro et al. 2014) but measuring whether this influence is positive or negative at the community scale is challenging. Increased visitation due to an attractive neighbour will likely benefit pollen limited species (Laverty 1992, Johnson et al. 2003) but, if stigmas get clogged by hetero-specific pollen, the net effect of co-occurring with attractive neighbours could be detrimental to the focal plant (Fang and Huang 2013). That said, stigma clogging by attractive neighbours is not inevitable (*e.g.* Emer et al. 2015) and the overall impact of adding plants to communities will be truly understood when seed-set and recruitment are measured.

While central species were attractive to pollinators, their introduction did not increase network centralisation as expected (Aizen et al. 2008, Bartomeus et al. 2008). On the other hand, the introduction of peripheral species decreased centralisation and interaction evenness. Introduced central species may have simply replaced the previous central species present in the subplots maintaining network centralisation, while peripheral species by occupying similar network roles of resident species (Fig. 4a-b) promoted networks with lower centralisation. The similar evenness observed for control and central networks agrees with results at the species level: central species presented high levels of partner diversity (Fig. 4b) without affecting visitation to resident species. This suggests that the high and even visitation received by central species was not obtained at the expense of resident species. In antagonistic networks, perturbations such as habitat modification and species invasions have been associated with both decreased (Tylianakis et al. 2007) and increased (Lopez-Nunez et

al. 2017) interaction evenness. In contrast, interaction evenness was unaffected by an invasive plant species in pollination networks (Tiedeken and Stout 2015). The effect of interaction evenness on community functioning and stability is not fully understood: while evenness of species abundance is often associated with enhanced community functioning and resilience (Hillebrand et al. 2008, Crowder et al. 2010), theoretical work suggests that the presence of weak interactions in the network has a stabilising effect (McCann et al. 1998, Berlow 1999). Looking forward, further work is needed to elucidate how levels of interaction evenness are associated with community functioning and persistence over time.

Conclusion

Our study is an initial step in the potential use of ecological networks as a tool for improving restoration decisions. Despite its small scale, our study suggests that network metrics are able to capture information on species ecological roles. Given that most restoration projects begin at the plant community (Montoya et al. 2012), being able to select the plants with the highest potential to promote community-level properties would be very useful. For instance, robustness and resilience are key network statistics in successful conservation (Mace 2014), and species network roles could be used to identify the most likely plants to promote these properties. As our knowledge about the structure and dynamics of ecological networks increases, more field experiments are needed to test our understanding of the parameters we identify and measure. For instance, future studies should use indices that account for interaction frequency between species, as these better capture information on species niche overlap and will bring new insights on species mutual dependence. Pollination networks are a good system for this approach, as they have been thoroughly studied (Bascompte and Jordano 2007, Burkle and Alarcón 2011), they are straightforward to manipulate (*e.g.* Brosi and Briggs 2013) and are under severe threat (Santamaría et al. 2016).

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Supplementary material (available online as Appendix oik-06183 at <www.oikosjournal.org/appendix/oik-06183>). Appendix 1.

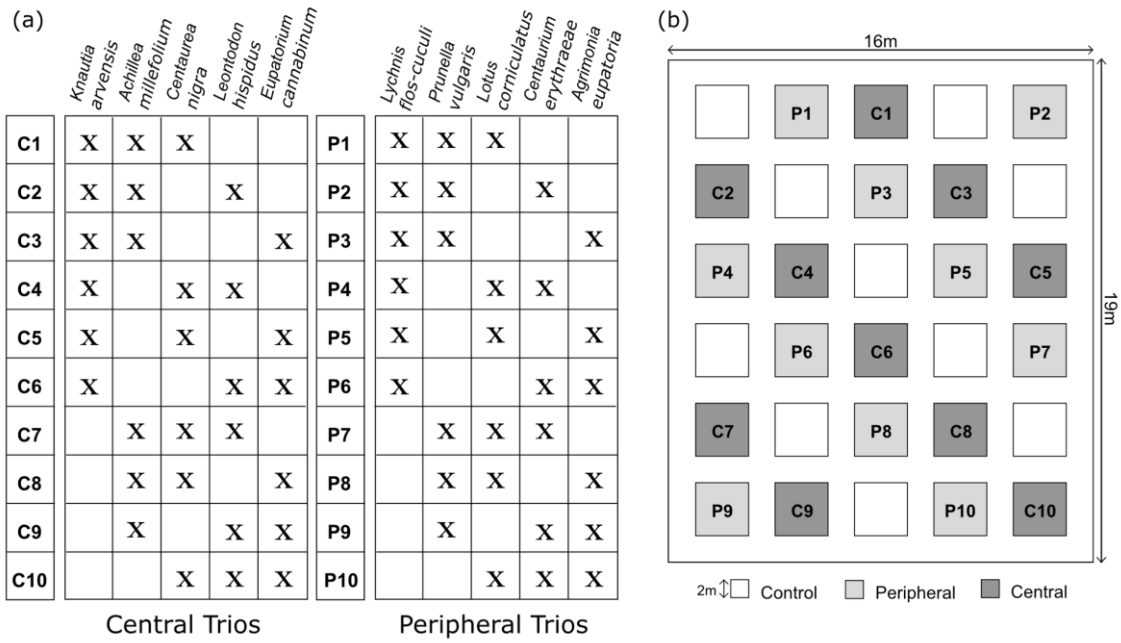
(a)
Knautia arvensis
Achillea millefolium
Centaurea nigra
Leontodon hispidus
Eupatorium cannabinum
Lychnis flos-cuculi
Prunella vulgaris
Lotus corniculatus
Centaurium erythraeae
Agrimonia eupatoria
C1 X X X
C2 X X X
C3 X X X
C4 X X X
C5 X X X
C6 X X X
C7 X X X
C8 X X X
C9 X X X
C10 X X X
P1 X X X
P2 X X X
P3 X X X
P4 X X X
P5 X X X
P6 X X X
P7 X X X
P8 X X X
P9 X X X
P10 X X X
Central Trios
Peripheral Trios
(b)
16m
19m
P1 C1 P2
C2 P3 C3
P4 C4 P5 C5
P6 C6 P7
C7 P8 C8
P9 C9 P10 C10
2m
Control
Peripheral
Central

Figure 1

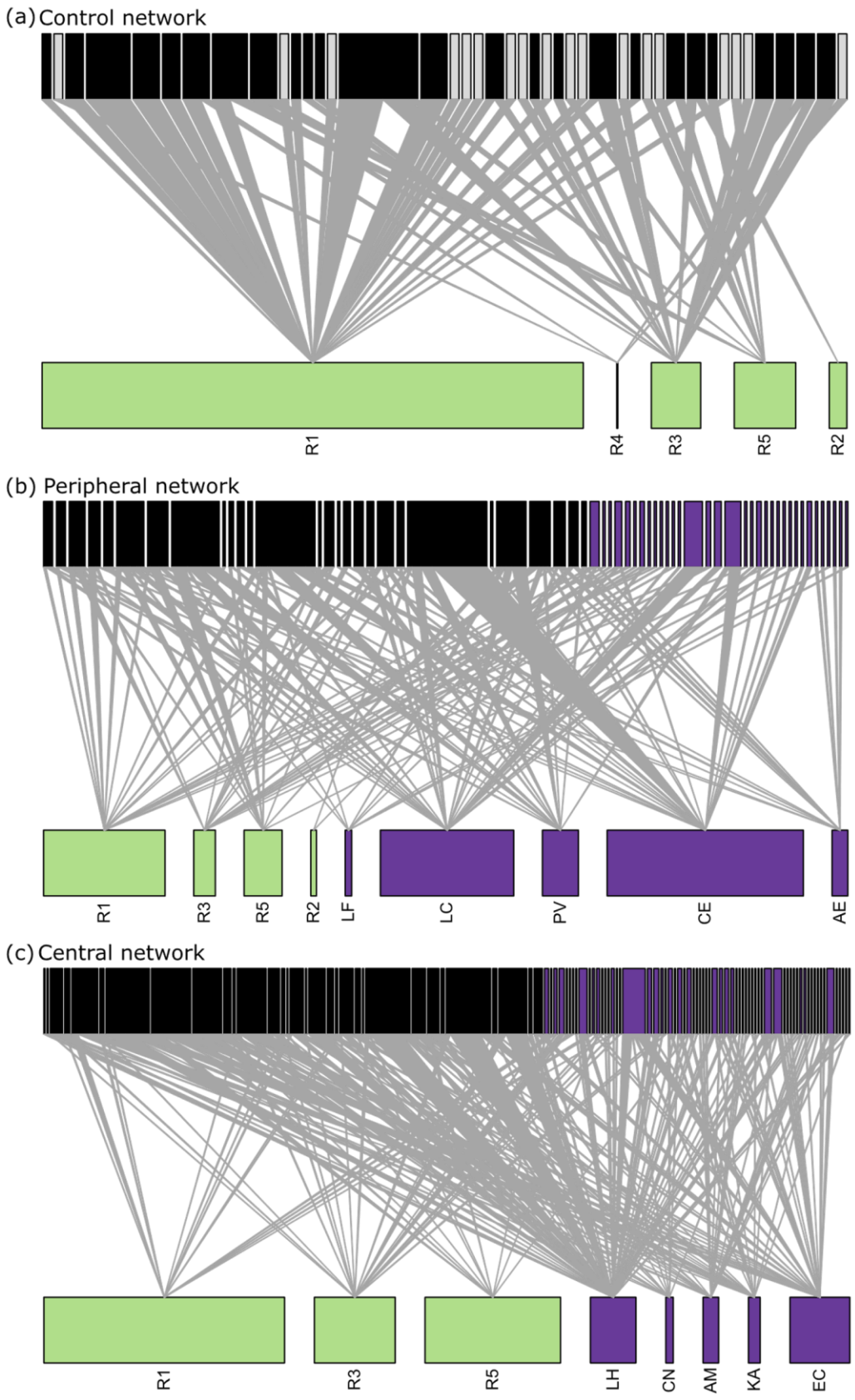
(a) Control network
R1
R4
R3
R5
R2
(b) Peripheral network
R1
R3
R5
R2
LF
LC
PV
CE
AE
(c) Central network
R1
R3
R5
LH
CN
AM
KA
EC

Figure 2

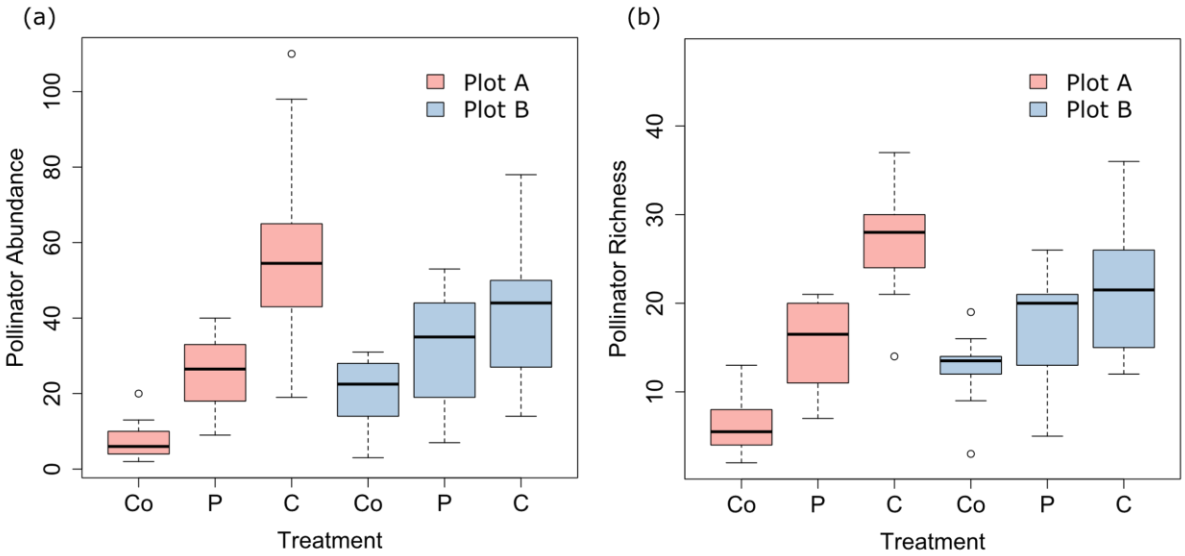
(a)
Pollinator Abundance
0
20
40
60
80
100
Plot A
Plot B
Co
P
C
Co
P
C
Treatment
(b)
Pollinator Richness
10
20
30
40
Plot A
Plot B
Co
P
C
Co
P
C
Treatment

Figure 3

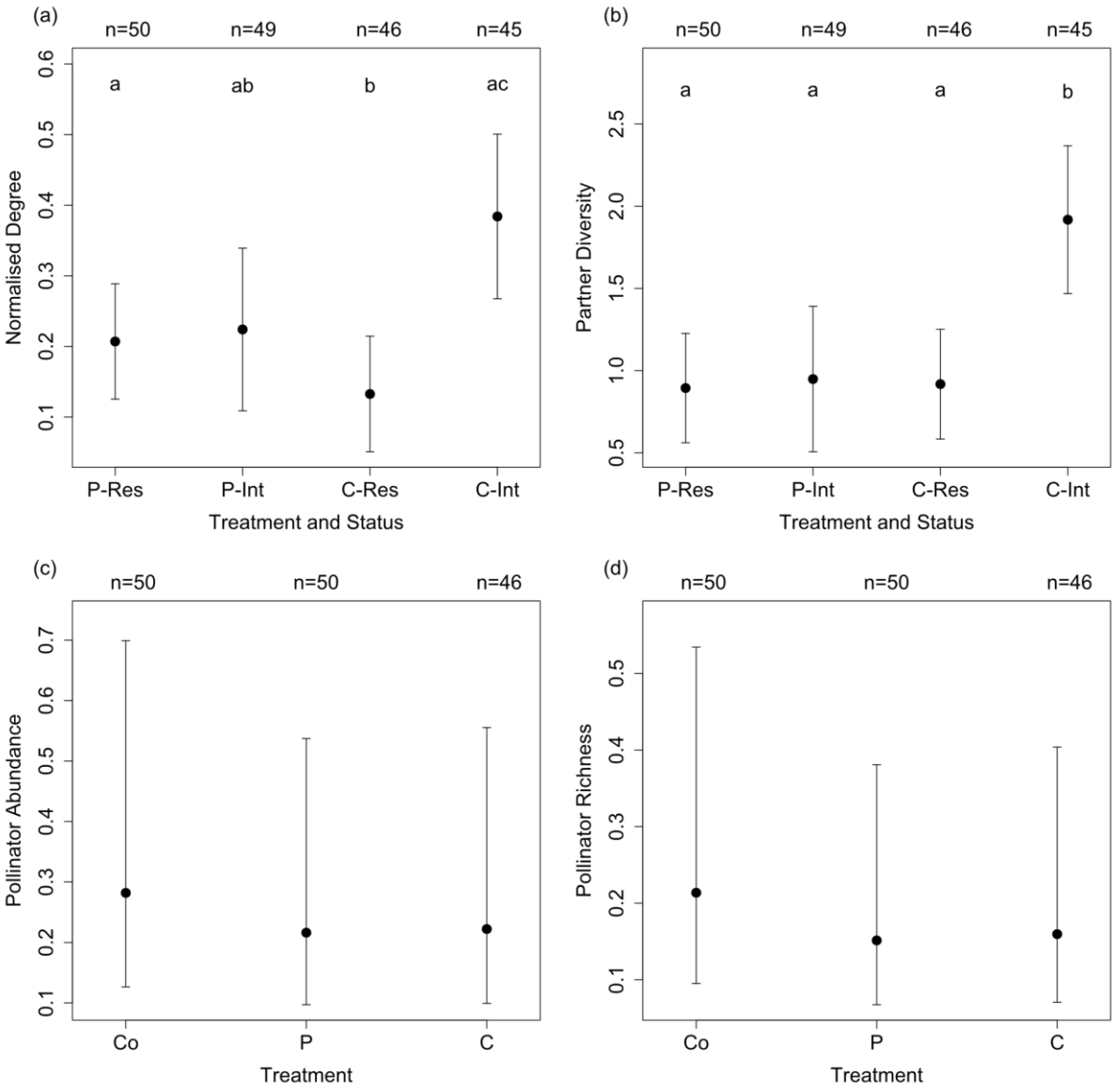
(a)
n=50
n=49
n=46
n=45
a
ab
b
ac
Normalised Degree
0.1
0.2
0.3
0.4
0.5
0.6
P-Res
P-Int
C-Res
C-Int
Treatment and Status
(b)
n=50
n=49
n=46
n=45
a
a
a
b
Partner Diversity
0.5
1.0
1.5
2.0
2.5
P-Res
P-Int
C-Res
C-Int
Treatment and Status
(c)
n=50
n=50
n=46
Pollinator Abundance
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Co
P
C
Treatment
(d)
n=50
n=50
n=46
Pollinator Richness
0.1
0.2
0.3
0.4
0.5
Co
P
C
Treatment

Figure 4

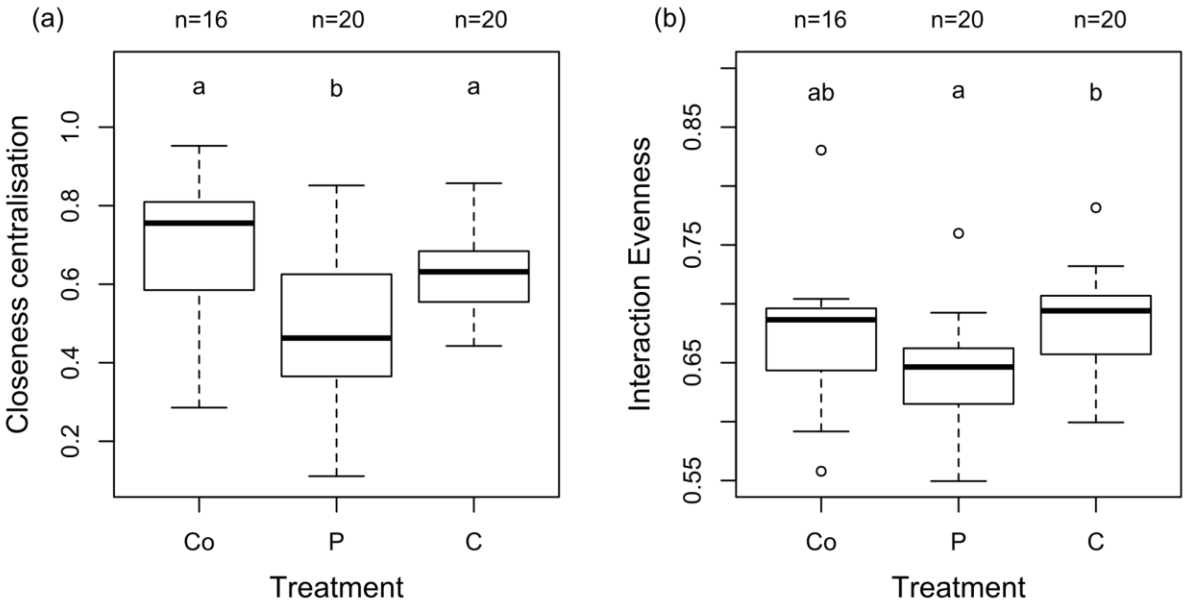
(a)
n=16
n=20
n=20
a
b
a
Closeness centralisation
0.2
0.4
0.6
0.8
1.0
Co
P
C
Treatment
(b)
n=16
n=20
n=20
ab
a
b
Interaction Evenness
0.55
0.65
0.75
0.85
Co
P
C
Treatment

Figure 5

Figure captions

Figure 1. (a) Ten trios of central (C1 to C10) and peripheral (P1 to P10) plant species; central species: *Knautia arvensis*, *Achillea millefolium*, *Centaurea nigra*, *Leontodon hispidus*, and *Eupatorium cannabinum*; peripheral species: *Lychnis flos-cuculi*, *Prunella vulgaris*, *Lotus corniculatus*, *Centaurium erythraea* and *Agrimonia eupatoria*. Species belonging to each trio are marked with an X. (b) Experimental plot: white squares represent control subplots, light grey squares represent peripheral subplots (P1 to P10) and darker grey squares represent central subplots (C1 to C10). Plant trios from P1 to P10 and C1 to C10 (Figure 1a) were planted in the corresponding peripheral and central subplots.

Figure 2. Quantitative pollination networks of (a) control, (b) peripheral and (c) central treatments of Plot A (see Figure A3 for Plot B). The networks show interaction data pooled across all subplots for each treatment in this plot, although analyses were conducted on a per-subplot-per-plot basis. For each network, the lower rectangles represent plant species abundance, the upper rectangles represent insect species abundance and link widths represent interaction frequency between species pairs. In purple are the introduced plant species along with the insect species which only appear in peripheral and/or central subplots. In light grey (control network) are insect species only observed in control subplots. Codes for introduced plant species: *KA=Knautia arvensis, AM=Achillea millefolium, CN=Centaurea nigra, LH=Leontodon hispidus, EC=Eupatorium cannabinum, LF=Lychnis flos-cuculi, PV=Prunella vulgaris, LC=Lotus corniculatus, CE=Centaurium erythraea, AE=Agrimonia eupatoria*. Resident species were numbered from R1 to R5 and names are given in Supplementary material Appendix 1, Table A3.

Figure 3. (a) Pollinator abundance and (b) pollinator species richness in both experimental plots (Plots A and B). Boxes show the first and third quartiles (lower and upper limits) and the median (midline).

Figure 4. Network roles (model estimates and confidence intervals) of resident and introduced species in peripheral and central networks: (a) normalized degree and (b) partner diversity. P-Res and P-Int are resident and introduced species in peripheral networks, and C-Res and C-Int are resident and introduced species in central networks. Insect visitation (model estimates and confidence intervals for Plot A) to resident species in control (Co), peripheral (P) and central (C) networks: (c) pollinator abundance and (d) pollinator richness. Different letters represent statistically different treatments.

Figure 5. Network-level structure of plant-pollinator interactions across treatments. (a) closeness centralisation and (b) interaction evenness. Different letters represent statistically different treatments. Boxes show the first and third quartiles (lower and upper limits) and the median (midline). Code for treatment: Co=control, P=peripheral, C=central.

Table 1. Effect of plant introduction (treatments=control, peripheral and central) and plant richness on the abundance and richness of pollinators. Untransformed model coefficients (Coef.), standard errors (SE), z- and P-values, and back-transformed estimates (Est.), lower and upper limits of 95% confidence intervals (2.5% and 97.5%, respectively).

Pollinator abundance							
	Coef.	**SE**	**z-value**	**P-value**	**Est.**	**2.5 %**	**97.5 %**
Control	-2.58	0.14	-18.04	<0.001	0.08	0.06	0.10
Peripheral	-3.07	0.15	-21.02	<0.001	0.05	0.03	0.06
Central	-1.62	0.13	-12.09	<0.001	0.20	0.15	0.26
Richness	-0.14	0.03	-5.02	<0.001	0.87	0.82	0.92
Pollinator richness							
	Coef.	**SE**	**z-value**	**P-value**	**Est.**	**2.5 %**	**97.5 %**
Control	-2.61	0.15	-18.03	<0.001	0.07	0.05	0.10
Peripheral	-3.18	0.15	-21.10	<0.001	0.04	0.03	0.06
Central	-1.76	0.14	-12.85	<0.001	0.17	0.13	0.23
Richness	-0.14	0.03	-4.83	<0.001	0.87	0.82	0.92