

STRUCTURAL CONTROLLABILITY OF POLLINATION NETWORKS

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Abstract

Si sabemos que el disfrute exige lentitud, y que—mas en general—la felicidad se asocia con el ir despacio, por que corremos tanto? El arte de comer estriba en saborear cada bocado sin pensar en el siguiente, sin apresurar el siguiente. El arte de leer, en demorarse en cada palabra como si el sentido del escrito entero estuviera contenido en ella. El arte de amar, en vivir cada momento de la relacion con la persona amada como si fuese el destino de toda la historia del mundo, desde la aparicion del primer organismo unicelular hasta hoy. Y asi podemos generalizar a las demas actividades, creo, hasta obtener un arte de vivir. Para mi se resume en la palabra ahi. — Jorge Riechmann

Keywords— Control theory, box in the article

Introduction

Ecological communities are formed by the interconnection of several species. Therefore, changes in the abundances of one species can potentially alter the abundances of the species they interact with. For instance, in a classic example of ecosystem cascades, a reduction on the abundance of sea otters, an important predator or sea urchins, can drive a dramatic reduction on kelp abundances because the sea urchins that consume kelp are released from predation. It has been long established that some species, like the sea otter, have a disproportionate large effect in their environment relative to their abundance.

In several ecosystems the relative importance of species have been identified based on empirical observations of long term dynamics. However, in less studied, highly diverse, or where the "keystone" role is shared by several species, it can be challenging to determine which is the set of species that influence the most the ecosystem dynamics. Alternative approaches that recognize a continuum of importance and that are less dependent on empirical observations have also been developed. Some of them are based on metrics that evaluate their position in the food web or on mass balance models of functional groups. Nevertheless, these approaches are conceptually limited to trophic interactions and in general ignore the structural mechanisms that allow or prevent the spread of perturbations in the ecosystem.

From a systems perspective, perturbations like over-exploitation, eutrophication or global warming are equivalent to management actions like culling, no-take areas or captive rearing in the sense that they have the potential to modify the abundances of one or several species in the ecosystem. Therefore identifying these key species is crucial not only to predict how these perturbations will spread trough the community but also to guide effective conservation efforts.

Recent work on the control of complex systems suggest that in principle it is possible to alter any ecological community's composition, by modifying the abundances of just some key species (Isbell and Loreau 2013; Cornelius, Kath, and Motter 2013). Here, we apply these theories to estimate the controllability of different

ecological communities and to find driver species: species, that due to the structural characteristics of their interactions are more likely to drive the dynamics of the community.

Invasive species have been shown to have a disproportionate effect on the structure of pollination communities. Influencing for example the strength of species interactions, and the degree of network nestedness and connectivity (Olesen, Eskildsen, and Venkatasamy 2002; Aizen, Morales, and Morales 2008; Bartomeus, Vilà, and Santamaría 2008; Vilà et al. 2009; Traveset et al. 2013). However whether this influence is translated into a driver role has not been tested. Here we use plant pollinator communities to investigate the number of species that should be managed to control population dynamics of the whole community, the characteristics that determine whether a species should be managed or not and how invasive species fit.

Methods

To investigate the dynamic controllability of pollination networks, we used data from ten paired plant-pollinator communities. Each pair was composed by a community invaded by a plant and a community effectively free of the invasive species (Table S1). The networks were constructed from previously published pollination visitation data collected from pollination communities in Bristol, UK (Lopezaraiza-Mikel et al. 2007) and Cap de Creus National Park, Spain (Bartomeus, Vilà, and Santamaría 2008). In the four British uninvaded communities the non-invaded plots were obtained by experimentally removing all the flowers of invasive species *Impatiens grandulifera*. In contrast, the Spanish uninvaded communities were obtained from plots that had not yet been colonised by the invasive species *Carpobrotus affine acinaciformis* or *Opuntia stricta*.

All analysis were performed in R 3.2.2 using bipartite 2.05, igraph 1.0.1, lme4 1.0-6, MuMIn 1.15.6, and vegan 2.3-3 (R Core Team 2015; Dormann, Gruber, and Fründ 2008; Csardi and Nepusz 2006; Bates et al. 2014; Barto 2016; Oksanen et al. 2016).

Manageability

Changes on the abundances of a species can modify the abundances of those species it interacts with. We exploit this concept to quantify the *manageability* of an ecological community (Equation 1). Manageability is directly related to the minimum number of species on which we would need to apply management interventions if we were to gain full control of the abundances of all species in the ecological community, n_d . We calculated n_d by finding the maximum matching of the pollination network in each community (Box 1).

$$m = 1 - \frac{n_d}{n} \quad (1)$$

We assumed that for a pair of interacting species the direction of control is inverse to the direction of dependency. If, for instance, a plant species depends more on a pollinator species than the pollinator depends on the plant, we expect the plant abundances to be more sensitive to changes in the pollinator abundance than vice versa. However, our results are robust to this assumption as its violation renders qualitatively consistent results (Figure S1 and S2; Table S2). Therefore, we first assigned a single direction to each link between plants and pollinators based on the direction the asymmetries in dependencies based on visitation frequencies following Bascompte, Jordano, and Olesen (2006). The dependency of plant i on pollinator j is the proportion of the visits coming from pollinator j compared to all pollinator visits to plant i . Likewise, the dependency of pollinator j on plant i is the ratio of the visits by pollinator j to plant i and all visits of pollinator j .

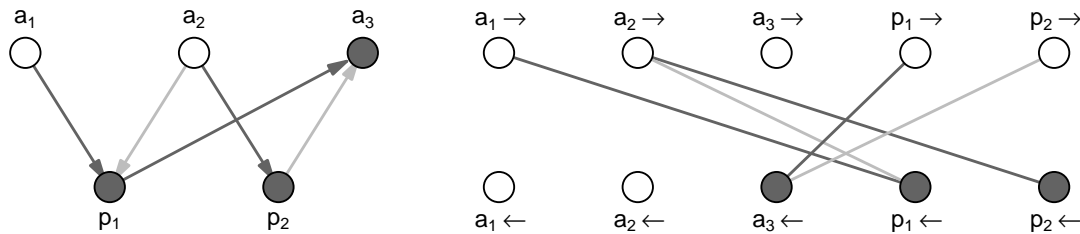
Intuitively, there is a relationship between diversity and manageability. We therefore used a set of

need ecological justification; why is n_d a good metric?

really? maybe Jason can help with a citation? or is there a better justification?

Box 1: Maximum matching

It has been shown that the number of nodes (here species) necessary to fully control a complex network, can be calculated by counting the number of unmatched nodes (Liu, Slotine, and Barabási 2011). In a directed network, like the simple pollination network shown on the left, a matching is a subset of links in which no two links share a common starting species or a common ending species—dark grey links—and a node is matched if it is the ending node of one of the links in the matching—dark grey nodes (West 2001).



To find the maximum matching we used a bipartite representation of the network, like the one on the right, in which the levels indicate the outgoing and incoming links to each node. Finding a matching here is equivalent to finding the links such that each node on the top is matched to at most one node on the bottom and vice versa (West 2001). The maximum matching is the one in which the matched links have the largest possible weight among all possible matchings.

The use of a maximum matching has also an intuitive explanation. In control theory lingo, a network is fully controllable when each node in the network has a "superior" or input that drives its dynamics. Matched nodes can be controlled within the network by the node pointing to it—its superior. However, unmatched nodes have no superior in the network and must be directly controlled by external inputs—what we refer to as management interventions (Liu, Slotine, and Barabási 2011).

The size of the maximum matching is therefore directly related to its *manageability* because systems that require a large number of inputs are more difficult to control. The manageability of the shown network is $m = 0.6$ because in theory, it is possible to guide the community to a desired state by applying management interventions to two of the five species in the community ($n_d = 2$; a_1 and a_2 in the depicted maximum matching).

generalised linear models to investigate the relationship between community manageability and (i) the total number of species, (ii) plant richness, (iii) pollinators richness, and (iv) the ratio of plants to pollinators richness. Because both invaded and British communities tend to be more diverse, we also assessed whether observed differences in manageability were due to these two factors.

To quantify the extent to which the manageability of a pollination community is characteristic of the network structure, we compared it to a suite of random null-models. An initial set of null models was based on network randomisations that maintained the species degree (the number of interactions), or that maintained the species strength (total sum of interaction weights). Subsequently we calculated the dependencies followed by the manageability of the randomised networks. A second set of null models was based on randomisations that maintained the structure of the empirical network but randomised the direction of dependencies between species. In all cases we calculated a Z-score between the manageability of each empirical network and the corresponding manageability of 999 randomisations.

Driver species

The manageability of a community, m , provides an indication of the magnitude of n_d but not the identity of the species that can compose this set. In fact maximum matchings are not unusually unique in ecological

networks and different sets of species of size n_d could be used to control the network (Liu, Slotine, and Barabási 2011). Nevertheless, species vary on the frequency at which they are part of this set; an indication of their relative importance to drive the state of the ecosystem.

We therefore call *driver species* those that are identified as needing directed interventions in the majority of maximum matchings, and therefore likely to have a disproportionate effect on the abundances of other species in the community. We identified the driver species in each of the communities by computing all possible maximum matchings in the network. To do so, we first generated the network's line graph—an alternative representation in which nodes are the interactions of the original network and links represent common ending points. We then calculated the complement of the line graph—a graph in which nodes are adjacent if and only if they are not adjacent in the line graph. All possible maximum matchings can be found by enumerating all cliques of size $1 - n_d$ in the complement graph (West 2001).

We then tackled the question whether some species level structural properties can predict the relative importance of driver species. Here, we evaluated the effect on the species' relative importance of measures of centrality (degree, betweenness, and overlap), measures related to network robustness (contribution to nestedness), and measures of strength of association (visitation levels). Candidate models were compared using AIC and the relative importance of the explanatory variables was evaluated using the sum of Akaike weights over all candidate models (Burnham and Anderson 2003).

Visitation as a proxy for species interdependence

Visitation frequency has been shown to be an appropriate surrogate for inter-specific effects in pollination networks (Vázquez, Morris, and Jordano 2005; Bascompte, Jordano, and Olesen 2006). Arguably, visitation reflects adequately the dependency of animals to plants, as usually during a visit animals forage for pollen or nectar regardless of whether effective pollination occurs. Nevertheless visitation is not equivalent to pollen deposition and might be insufficient to reflect the dependencies of plants on animals (Alarcón 2010; King, Ballantyne, and Willmer 2013). We therefore investigated the effect of calculating the dependencies using pollination effectiveness and importance—two metrics more proximate to plant reproductive success.

any citation
Daniel?

Pollinator efficiency is measured as “the number of conspecific pollen grains deposited on a virgin stigma during a single visit by a particular animal” (Ne'Eman et al. 2010). Pollinator importance on the other hand is defined as the product between visitation frequency and pollinator efficiency (Ballantyne, Baldock, and Willmer 2015). We used data collected by Ballantyne, Baldock, and Willmer (2015) from a low diversity pollination community at a dry lowland heathland in Dorset, UK. We assessed the differences between visitation, pollinator effectiveness, and pollinator importance by comparing (i) the manageability of the community, (ii) the percentage of interactions that maintained the direction of dependency, and (iii) the Spearman correlation of the relative importance of the species in the community.

Results

Manageability

We found that if we were to control the dynamics of the whole community, we would need to control between 55 and 92% (mean 76%) of the species in the community—which corresponds to manageabilities of 0.08 to 0.45 (Table S1). In addition we found that the ratio of plant to pollinator species richness had an important positive effect on the community manageability ($Pr(> \chi^2) = 0.007$). Contrastingly measures of biodiversity (like plant or pollinator richness) or factors such as the status of invasion, or the location of the study did not have a significant effect on the manageability (Figure 1, Table S3).

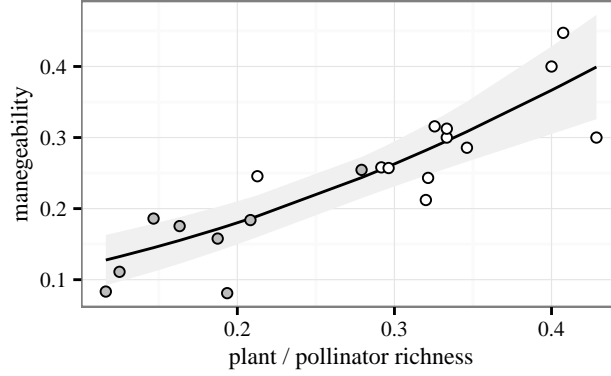


Figure 1: The proportion of species needed to control the network is largely influenced by the ratio of plant to pollinator species richness but not the location of the community. White dots correspond to communities investigated by Bartomeus, Vilà, and Santamaría (2008); grey dots correspond to communities investigated by Lopezaraiza-Mikel et al. (2007).

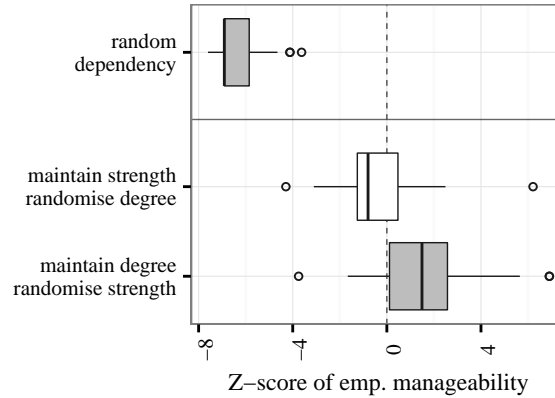


Figure 2: The manageability of empirical networks is much smaller than those of network randomisations in which the direction of dependencies has been randomised. In contrast the manageability of network randomisations that maintain the strength or the degree of species. The grey filling indicates that the Z-score is significantly different from zero (t-test, $p < 0.05$).

We found that the manageability of empirical networks varied little when compared to network randomisations that maintained the species strength or species degree (two tailed t-test, $p = 0.457$ and 0.011 respectively; Figure 2). This results were also broadly consistent with those obtained including both dependencies (Figure S3). Contrastingly, empirical networks have are much harder to manage than network randomisations in which the direction of the dependencies is altered but the structure is maintained.

Driver species

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factor	est.	No. mod.	imp.	C.I.	factor	est.	No. mod.	imp.	C.I.
d	-1.58	67	1.00	0.81	$d : S_d$	1.78	86	1.00	1.58
$d : S_d$	4.71	67	1.00	2.75	(Intercept)	-0.50	86	1.00	2.82
(Intercept)	3.59	67	1.00	1.12	S_d	-6.01	79	0.96	7.37
S_d	-10.45	67	1.00	5.76	d	-0.60	75	0.93	0.93
n	0.72	51	0.87	1.05	$n : S_d$	-1.25	40	0.54	3.73
$d : S_v$	0.12	38	0.72	0.24	$d : S_v$	0.10	39	0.51	0.27
$n : S_v$	-0.15	29	0.60	0.37	S_v	0.16	36	0.38	0.76
S_v	0.07	41	0.47	0.29	$S_d : S_v$	0.25	38	0.34	1.38
$d : n$	0.06	40	0.45	0.23	$d : n$	-0.02	31	0.30	0.09
$S_d : S_v$	-0.19	31	0.41	0.77	n	0.26	25	0.27	1.27
$n : S_d$	-0.28	29	0.32	1.58	$n : S_v$	0.08	26	0.26	0.41

(a) pollinators

(b) plants

Table 1: Minimum number and proportion of driver species necessary to control the full pollination network

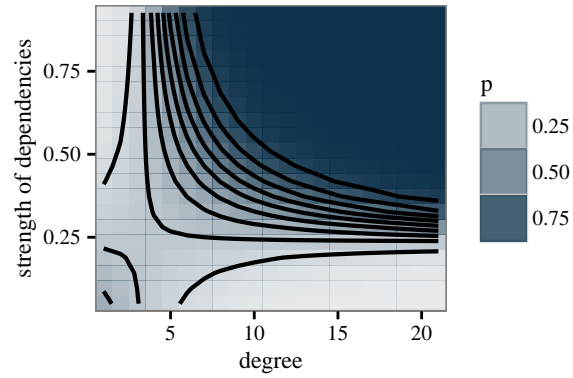


Figure 3: aSS

Author contributions

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Supplementary Information

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1 Manageability

We calculated the number of driver species necessary to control the whole community under the assumption that a species that depends more strongly on an interaction partner is controlled by the partner (Table S1). We tested the robustness of this assumption by comparing the relative number of driver species assuming that a) the dependency asymmetry does not imply an unidirectional control direction, rather a species could control all its interaction partners and vice versa, b) that plants depend on pollinators and c) that pollinators depend on plants (Figure S1). Our results using the direction of the largest dependency are consistent with the proposed alternatives: although we obtained different absolute numbers of driver species (Figure S2), their relative numbers are not statistically distinguishable (Table S2).

We built a set of three generalised linear models with a logistic error structure to investigate the variables that influence the set of driver species. We found that the proportion of driver species is largely independent of the study site but highly dependent on the ratio of plant to pollinator diversity (Table S3).

2 Driver species

Unlike unweighted networks, where a maximum matching is defined by its size (the number of matched edges), in weighted networks, a maximum matching is one whose edges have the largest possible total weight among all possible matchings. This means that in weighted networks there is a number of matchings that have maximal size, but are not maximum matchings because its total weight is not maximal too. Therefore, for weighted networks the number of possible maximum matchings, even for large networks, can be small (in the studied networks this number ranged from 1 to 48, $\bar{\mu} = 6.5$).

However the weight of species dependencies is unexact, a reflection of the fact that interaction strengths and sampling methods themselves are stochastic to some extent. This means that certain level of tolerance must be introduced so that we accept some matchings that have the same size but only a proportion of the maximum matching weight. As this proportion decreases we accept a markedly larger number of matchings (Figure S4).

site	invaded	No. pla.	No. pol.	n_d	manageability	source
1	no	9	26	25	0.29	Cap de Creus, Spain
1	yes	10	47	43	0.25	Cap de Creus, Spain
2	no	10	30	28	0.30	Cap de Creus, Spain
2	yes	11	27	21	0.45	Cap de Creus, Spain
3	no	7	24	23	0.26	Cap de Creus, Spain
3	yes	8	25	26	0.21	Cap de Creus, Spain
4	no	10	25	21	0.40	Cap de Creus, Spain
4	yes	14	43	39	0.32	Cap de Creus, Spain
5	no	8	27	26	0.26	Cap de Creus, Spain
5	yes	8	24	22	0.31	Cap de Creus, Spain
6	no	9	21	21	0.30	Cap de Creus, Spain
6	yes	9	28	28	0.24	Cap de Creus, Spain
7	no	6	31	34	0.08	Bristol, United Kingdom
7	yes	8	49	47	0.18	Bristol, United Kingdom
8	no	5	43	44	0.08	Bristol, United Kingdom
8	yes	15	72	71	0.18	Bristol, United Kingdom
9	no	12	43	41	0.25	Bristol, United Kingdom
9	yes	11	75	70	0.19	Bristol, United Kingdom
10	no	3	16	16	0.16	Bristol, United Kingdom
10	yes	6	48	48	0.11	Bristol, United Kingdom

Table S1: Properties of the analysed plant-pollinator communities. British networks were assembled by Lopezaraiza-Mikel et al. (2007), Spanish networks assembled by Bartomeus, Vilà, and Santamaría (2008).

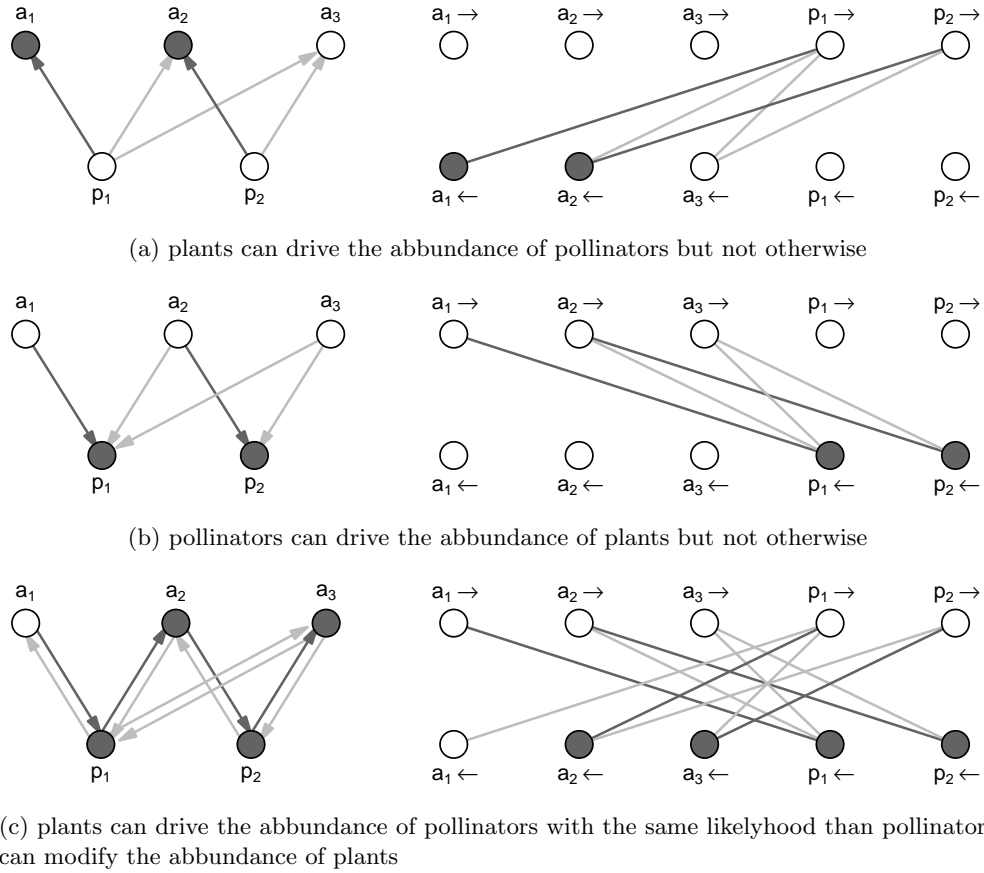


Figure S1: Here we show one of the possible maximum matching for each of the direction of control assumptions in the same simple plant pollinator network.

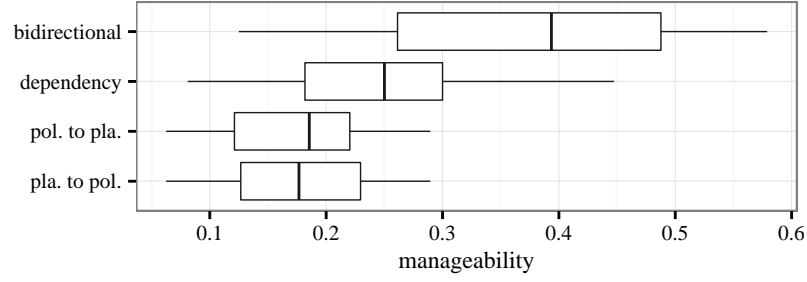


Figure S2: Proportion of driver species necessary to control the full pollination network under four different assumptions of the direction of control

	pol. to pla.	dependency	bidirectional
pla. to pol.	1	0.97	0.96
pol. to pla.		0.98	0.96
dependency			0.98

Table S2: Spearman correlation coefficients of the number of driver species necessary to control the full pollination network under the four different assumptions of the direction of control.

model	df	logLik	AICc	Δ AIC	weight
$m \sim r_{p/a}$	2	-43.11	90.94	0.00	0.50
$m \sim i + r_{p/a}$	3	-42.28	92.06	1.12	0.29
$m \sim r_{p/a} + s$	3	-42.97	93.45	2.51	0.14
$m \sim i + r_{p/a} + s$	4	-42.25	95.16	4.23	0.06
$m \sim s$	2	-47.19	99.09	8.16	0.01
$m \sim i + s$	3	-47.17	101.85	10.91	0.00
$m \sim i + s + n_p + n_a + n_p : n_a$	6	-42.40	103.26	12.32	0.00
$m \sim n_a$	2	-55.17	115.04	24.11	0.00
$m \sim n_p$	2	-55.91	116.53	25.60	0.00
$m \sim n$	2	-56.71	118.12	27.19	0.00
$m \sim i$	2	-58.94	122.59	31.65	0.00

Table S3: The manageability (m) is largely influenced by the ratio of plant to pollinator species richness ($r_{p/a}$) but not the location of the community (s), the plant richness (n_p), the pollinator richness (n_a), or the total number of species in the community (n). NOTE: In reality the response variable was $\text{cbind}(n_d, 1 - n_d)$, what's the convention to specify such a model?

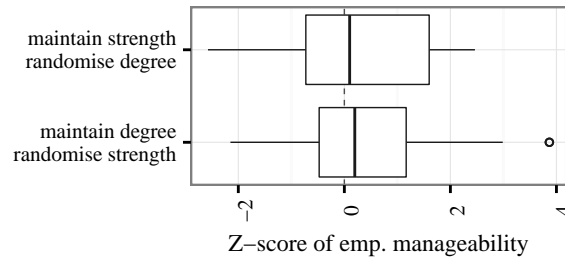


Figure S3: The manageability of network randomisations that maintain the strength or the degree of species is not different from the empirical manageability using bidirectional links.

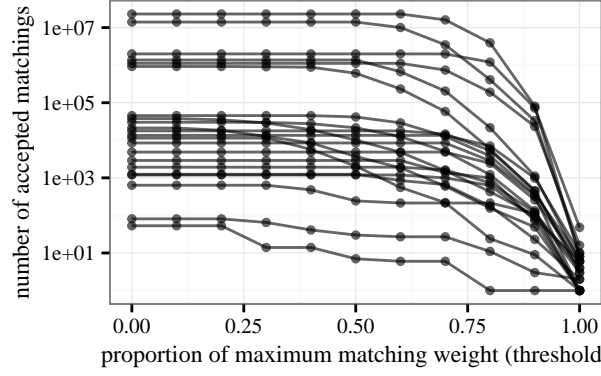


Figure S4: The number of accepted matchings increases as the proportion of maximum matching weight decreases. Each line correspond to one studied network.

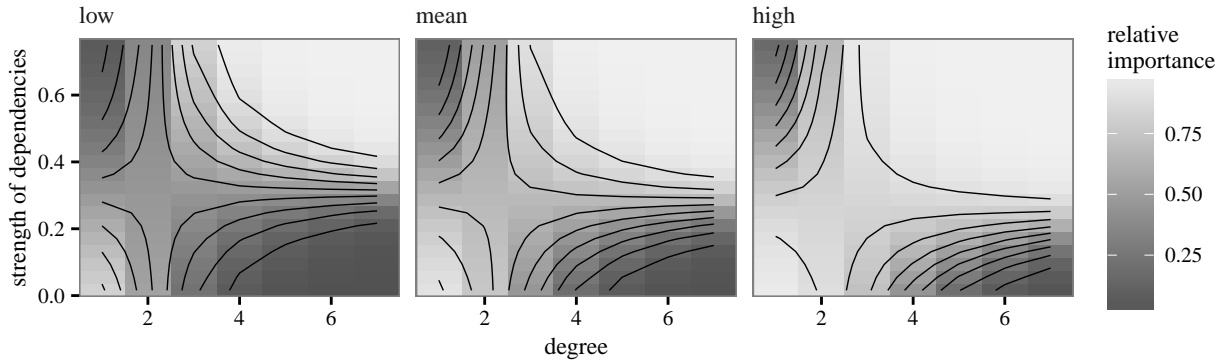
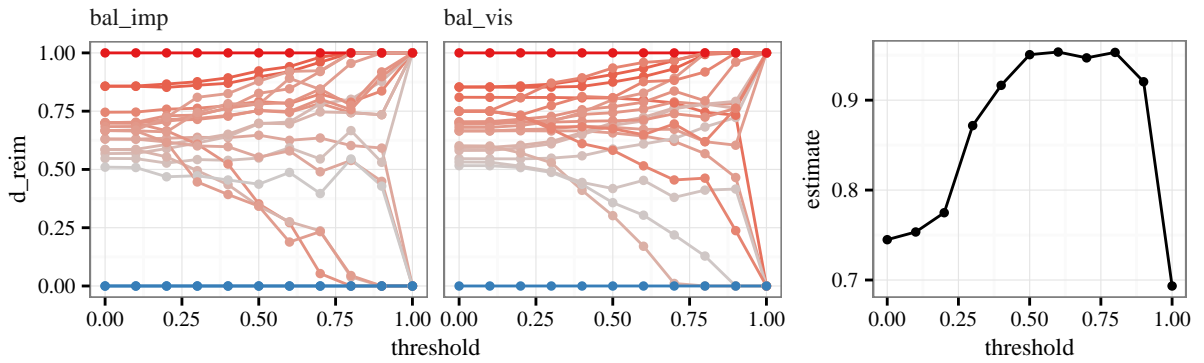


Figure S5: aSS



First we assessed the importance of each explanatory variable individually. We included the most relevant subset into a more detailed analysis that included first order interactions between them.

3 Visitation as a proxy for species interdependence

The number of driver species in a pollination community and the relative importance of each species depend both of the strength of mutual dependencies between plant pollinators and the structure of the pollination network. Traditionally pollination networks have been constructed on the basis of visitation frequency, but not all flower visitor are necessarily a pollinator. It has been shown that whether or not pollination networks

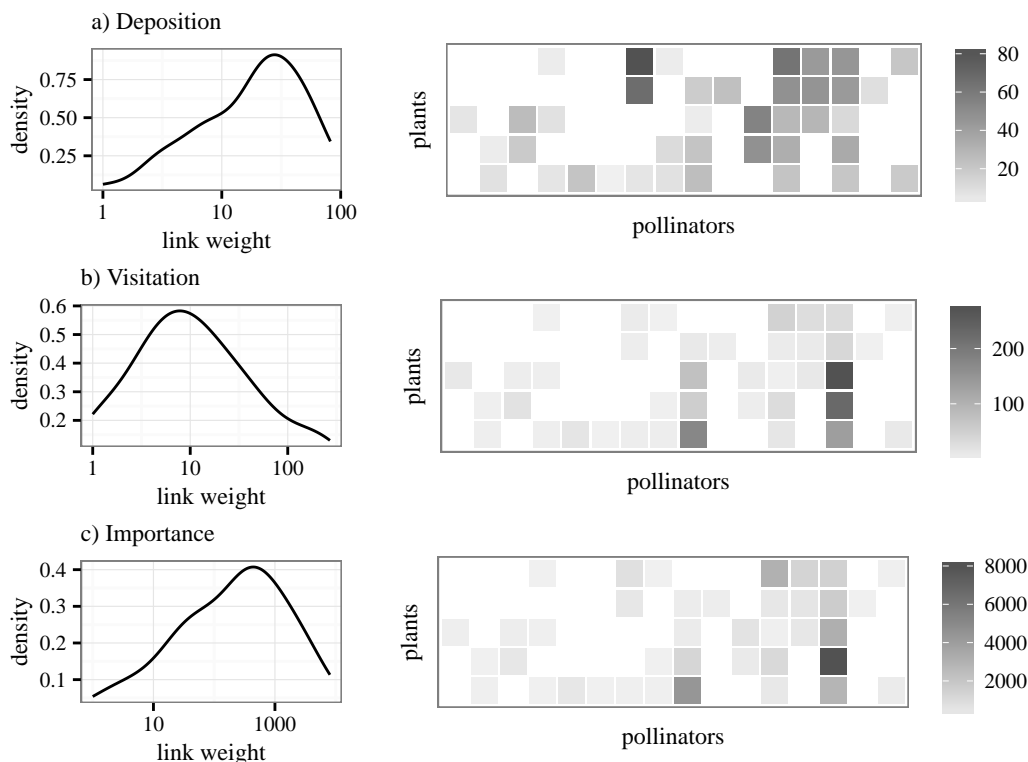


Figure S6: Distribution of interaction weights for the pollen deposition, visitation and pollinator importance networks. Note that the x axis in the density plots have been log-transformed

are represented using visitation or actual pollen deposition can have effects on the network structure and presumably on the strength of mutual dependency (Alarcón 2010).

We investigated the effects of using visitation, pollen deposition (effective pollination) and pollinator importance (the product of visitation frequency and effective single visit pollen deposition). We used available data collected by Ballantyne, Baldock, and Willmer (2015) from a low diversity pollination community at a dry lowland heathland in Dorset, UK (50 43.7'N 2 07.2'W).

Deposition networks were quantified using the mean Single Visit Deposition—the number of conspecific pollen grains effectively deposited on a virgin stigma during a single visit by a particular animal (Ne'Eman et al. 2010; King, Ballantyne, and Willmer 2013; Ballantyne, Baldock, and Willmer 2015). Visitation networks were constructed counting the visits to flowers during Single Visit Depositions. Pollinator importance networks were constructed as the product of pollinator efficiency and visit frequency.

We first investigated the effects at a network scale. Despite marked differences in the distribution of weights of the three networks (Figure S6), the minimum number of driver species to control the whole community was consistent among the three different approaches (0.33 for deposition, 0.33 for the visitation, and 0.38 for the pollinator importance network).

The choice of weighting used can also have an impact on the relative importance of species. Therefore we calculated the frequency that each species is present in the possible sets of driver species under the three schemes. Although visitation and deposition produce strikingly different results, we found a very strong agreement between the order produced by visitation and importance (Table S4). Arguably, visitation best reflects the dependency of animals to plants, as usually animals forage for pollen or nectar regardless of whether effective pollination occurs or not. Contrastingly, importance, the product between visit frequency and pollinator effectiveness, best reflects the dependency of plants to animals.

Finally, we investigated whether the asymmetry of mutual dependency, which defines the direction of

```
## Error in attr(x, "n_matchings") - x: non-numeric argument to binary operator
## Error in eval(expr, envir, enclos): object 'drivers.b' not found
## Error in combn(length(dir_net.b), 2): n < m
## Error in magrittr::set_colnames(., nam): length of 'dimnames' [2] not equal to array extent
```

Table S4: Spearman correlation coefficients (with p-value) of the relative importance of species and the percentage of interactions that share the direction of dependency obtained using the three weighting schemes and an unweighted scheme. Significant correlations are highlighted in bold.

control, was consistent among the three possible weighting schemes. We found again that the direction of the dominant dependency was maintained was consistent for 95% of the interactions weighted by visitation or importance (Table S4), the two most appropriate metrics for pollinator and plant dependency.

All together, evidence supports the idea that visitation is a suitable metric to estimate the mutual dependency of species pairs. First it is directly related to pollinator foraging. Second it produces results consistent, at least within our controllability framework, with plant reproductive success (as estimated by the importance metric).

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