

Quantifying the manageability of pollination networks in an invasion context

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Quantifying the manageability of pollination networks in an invasion context

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Abstract

1. Despite important advances in network ecology, the link between the structure of an interaction network and management or conservation is still tenuous. Perhaps in part because of a lack of theoretical framework, efforts to strengthen this link have been mainly focused on whole-network properties instead of underlying mechanisms.
2. Here, we leverage recent advances in control theory to develop an approach to assess the “manageability” of ecological networks. We then illustrate its application using ten pairs of uninvaded and invaded plant-pollinator communities. We also characterise species’ suitability for inclusion in management interventions by exploring the entire space of alternative control strategies. Specifically, we measure the extent to which species (i) are necessary to steer the state of the community and (ii) are able to affect the abundance of other species.
3. We found that the networks’ manageability is most strongly determined by the ratio of plant to pollinator richness, which in turn constrains the networks’ degree distribution. We also found that invasive plants have a dominant position in every invaded community and that this dominance is underpinned by high asymmetries in the dependences of their interaction partners.
4. *Synthesis.* Our results provide novel insight into the design of ecologically-informed management interventions and lay the foundation for further work on the control of ecological networks.

Keywords: Driver species, ecological networks, management interventions, mutualism, network control theory, plant population and community dynamics, species importance

Introduction

In a complex system, the whole is often greater than the sum of its parts (Montoya, Pimm & Sole 2006). Within community ecology, a complex-systems approach has led to the development of analytical and simulation tools with which to understand, for example, the role of species embedded in a network of interactions (Bascompte & Stouffer 2009; Stouffer *et al.* 2012). The inherent complexity of nature, however, has regularly hindered—or at least complicated—our ability to find management solutions to many problems ecological communities face. To overcome this obstacle, we require a framework that allows us to explain, predict, and manage ecological communities, particularly when they are confronted with perturbations (Green *et al.* 2005). Ideally, such a framework is equipped to account for their complex structure and the dynamics that determine the species abundances and the state of the community.

Among the various possibilities, *control theory* appears to be a strong candidate (Isbell & Loreau 2013). Widely used in engineering to determine and supervise the behaviour of dynamical systems (Motter 2015), it is well equipped to deal with the many feedbacks present in ecological communities (Liu & Barabási 2016). Research in this area has established a strong link between the structure of complex networks and their *controllability*—the relative ability to manipulate network components to drive the system to a desired state (Liu, Slotine & Barabási 2011; Cornelius, Kath & Motter 2013; Ruths & Ruths 2014). These advances suggest that it is in principle possible to alter a whole ecological community’s composition by modifying the abundances of only a few species. Applications of control theory to ecological networks can also take into account the extent to which changes in the abundances of one species may ripple through the community (Cornelius *et al.* 2013). Therefore, control theory could also be harnessed to help identify which species are most relevant from a structural and dynamic perspective.

This information is valuable not only for basic ecology, but it might be also relevant to address more applied management and conservation challenges. This is particularly true in the context of biotic invasions, where identifying key players in the community is a prerequisite to informed attempts to alter the state of invaded ecosystems and maintain the state of uninvaded ones. Despite recent advances in network theory, practical challenges to the conservation of interaction networks persist (Tylianakis *et al.* 2010), and the link between the structure of complex networks and our ability to manage and conserve them is still ambiguous (Blüthgen 2010; Kaiser-Bunbury & Blüthgen 2015). To complicate things further, biotic invasions can induce dramatic changes in the patterns of interactions that determine the structure of ecological networks (Tylianakis *et al.* 2008; Ehrenfeld 2010), in particular pollination (Olesen, Eskildsen & Venkatasamy 2002; Aizen, Morales & Morales 2008; Bartomeus, Vilà & Santamaría 2008; Vilà *et al.* 2009; Traveset *et al.* 2013). Understanding how the differences in network structure before and after invasion impact our ability to manage the communities is thus a double challenge, but it is also the critical first step towards a fully informed recovery. Despite the apparent overlap, the control-theoretic perspective

60 has not been adopted in an invasion context.

61 To bridge this gap, we outline an approach to apply control theory in an ecological context and implement
62 it using empirical data. Specifically, we use a set of ten pairs of uninvaded and invaded plant-pollinator
63 communities to investigate the link between invasion, network structure and ecological management.
64 While doing so, we focus on two particular questions. First, grounded in the difficulties usually involved
65 with invasive-species eradication and ecosystem restoration (Woodford *et al.* 2016), we ask whether
66 invaded networks have lower levels of “manageability” than their uninvaded counterparts; that is, whether
67 they require a greater proportion of species to be managed to achieve the same level of control. Second,
68 we ask whether some species are more important than others at driving the population dynamics of the
69 community and which factors determine this importance.

Theoretical framework

70 At the core of representing ecological communities as complex systems sits the idea that the state of
71 any given node depends on its state, the state of the nodes it interacts with, the state of the nodes they
72 interact with, and so on. These dependencies are given by the structure of the interactions, the dynamic
73 relationships between nodes, and the mechanisms of self-regulation. This representation has been very
74 useful for our understanding of ecological communities and might be advantageous for a more formal
75 approach to ecological management based on control theory.

76 The overall objective of control theory is to be able to steer a system from one state to another in finite
77 time. However, in complex systems like ecological communities, the large number of nodes and interactions
78 as well as their non-linear dynamics render its control extremely challenging. On one theoretical extreme,
79 for instance, any ecological community could be fully controlled if we control the state of every species
80 independently. On another, the mechanisms of self-regulation and the multiple feedback cycles found
81 in ecological communities mean it is also theoretically possible to control the whole community by
82 directly modifying the state of just a *single* species (Rahmani *et al.* 2009; Cowan *et al.* 2012). Although
83 mathematically correct, neither of these options are practical in real-world applications: the first because
84 it is infeasible to design and implement interventions that modify the abundance of every single species
85 in a community, and the second because the control signal might require unreasonably large amounts of
86 time, energy, or unattainable rapid changes on the state (Yan *et al.* 2012; Motter 2015). Here we explore
87 an intermediate point between these two trivial solutions.

88 In particular, we leverage the principle of species interdependence to find an intermediate set of *driver*
89 *nodes* to control the network (Liu & Barabási 2016). When we focus on net interspecific effects, it is

possible to identify a minimum number of nodes the control of which can theoretically drive the state of every other node in the network to a desired configuration. Conveniently the information necessary to determine this minimum number of driver nodes D is fully contained in the network structure (Kalman 1963; Liu *et al.* 2011; Motter 2015). Such a system can be described by $\frac{dx}{dt} = \mathbf{A}x + \mathbf{B}u(t)$, where the change of its state over time ($\frac{dx}{dt}$) depends on its current state x (for example, the species' abundances), an external time-varying input $u(t)$ (the control signal), and two matrices \mathbf{A} and \mathbf{B} , which encode information about the network structure and how the species respond to the external input, respectively. If S is the number of species in the community, the matrix \mathbf{A} has size $S \times S$ whereas the matrix \mathbf{B} has size $S \times D$. The goal of structural controllability, which we employ here, is to use the information contained in \mathbf{A} to generate a supportable estimate of \mathbf{B} (and by extension D). This focus allows us to gain insight of the inherent controllability of a network, and the roles of the species that compose it, without being overly dependent on the particular choices of how the system dynamics are modelled or characterised. The trade-off of our approach is that, because of the assumption of linearity, structural controllability alone does not allow us to fully design the time-varying control signal $u(t)$ that can drive the system from one particular equilibrium to another. Nevertheless, the lessons gained when assuming linearity—at both the network and the species level—are a prerequisite for eventually understanding nonlinear control (Liu *et al.* 2011; Liu & Barabási 2016).

Manageability

The number of driver nodes D provides a structural indication of how difficult a network's control might be. This is because systems that require a large number of external input signals are intuitively more difficult or costly to control. In an ecological context, external inputs that modify the state of a node can be thought of as management interventions. Therefore, the density of driver nodes $n_D = \frac{D}{S}$, where S is the total number of species in the community, is a measure of the extent to which network structure can be harnessed for network control. For instance, a hypothetical “network” in which species do not interact would require direct interventions for every single species to achieve full control, whereas a linear food chain would require just one species to be directly controlled to harness cascading effects through its trophic levels. From this perspective, it is possible to use n_D as an index of the manageability of an ecological community, understood in the context of how difficult is to modify the abundances of species in the community using external interventions—a common theme in ecosystem management, conservation, and restoration.

It has been recently shown that calculating D is equivalent to finding a maximum matching in the network (Liu *et al.* 2011). In a directed network, a *matching* consists of a subset of links in which no two of them share a common starting or ending node (Figure 1, Supporting Information S1). A given matching has

122 *maximal cardinality* if the number of matched links (also referred to as the *matching size*) is the largest
 123 possible. A maximal cardinality matching is then called a *maximum matching* if the sum of the weights
 124 of the matched links (also referred to as *matching weight*) is again the largest possible (West 2001).

125 Once we have the subset of links that constitute a matching, we can also classify the nodes in the network
 126 based on that matching (Figure 1). A node is called *matched* if it is at the end of a matched link and
 127 *unmatched* otherwise. A node is also called *superior* if it is at the start of a matched link. Note that a
 128 node cannot be superior if it has no outgoing links. Notably, these node categories are what helps us to
 129 link a maximum matching back to the concept of network controllability, as follows. Unmatched nodes are
 130 the *driver nodes* D because they have no superior in the network and must be directly controlled by an
 131 external input (Liu *et al.* 2011). Each matched node, on the other hand, can be controlled by its superior.

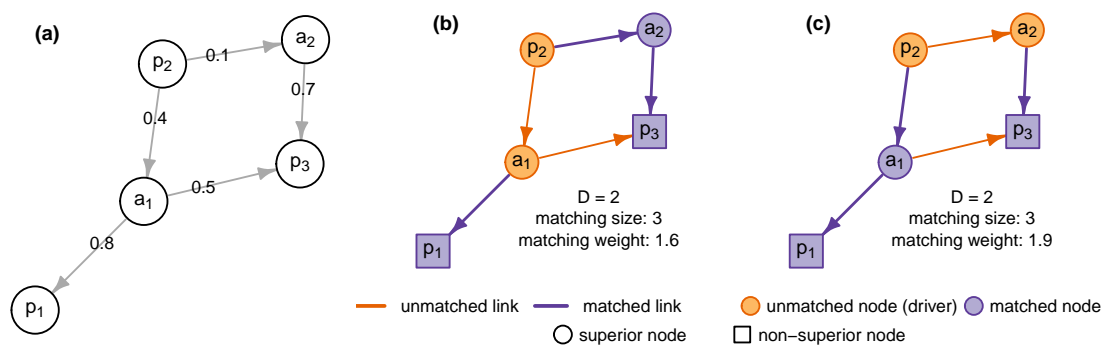


Figure 1: **Matchings of a simple network.** (a) We start with a network in which the direction of the links indicates the potential direction of control; for example a link from a_1 to p_1 indicates that the state of p_1 is influenced by the state of a_1 . The numbers indicate the weight of each link. (b & c) This network has two maximal cardinality matchings; that is, two configurations in which it would be possible to exert full control of the network via external input signals to a minimal set of nodes. In both cases, the three matched links (purple arrows) represent the control paths through the network and provide an indication of the matched nodes (purple), which are controlled by superior nodes within the network (circular nodes). Unmatched nodes (orange) are called driver nodes because full network control requires external signals to be applied to them. Out of the two maximal cardinality matchings only one (c) has maximum weight and therefore is also a maximum matching. Further examples can be found in Supporting Information S1.

132 Note that this framework requires a directed network in which the direction of the links corresponds to
 133 the direction of control. In the “Methods” section below, we explain our approach to determining the link
 134 direction in pollination networks.

Relative importance

135 While calculating n_D measures the manageability of an ecological community, it does not provide
 136 information about the identity of the species that compose the set of driver nodes. Ecologically, potential
 137 differences between species are relevant because management and conservation resources are limited, and
 138 therefore ecological interventions should be focused on the set of species that might provide the largest
 139 impact. Moreover, maximum matchings in a network are often not unique, and each maximum matching

indicates unique paths that can potentially be used to control the network. We harness this property and use a network's complete set of maximum matchings to characterise each species' relative importance in driving the state of the community. One possibility is to characterise a species by the frequency f_D with which it is classified as a driver node within this set of matchings. However, the profile of our networks indicates that a large proportion of species were classified as driver nodes because of external interventions required to achieve **full** controllability and not because they influence the abundance of other species (Supporting Information S2). Furthermore, the precise role of driver nodes is more ambiguous when full control is unfeasible or undesired—often the case in ecological settings. We therefore also calculate the frequency f_S with which a species is classified as a superior node since this is the frequency with which they form part of possible control paths.

Most commonly, structural controllability assumes unweighted networks—links exist or not, and hence f_D and f_S can be calculated by computing all possible maximum-cardinality matchings. However, we take the link weights into account when calculating the matchings here because the weights can reveal significant ecological patterns and processes that might be undetectable in unweighted networks (Scotti, Podani & Jordán 2007; Tylianakis, Tschardt & Lewis 2007; Vázquez *et al.* 2007; Kaiser-Bunbury *et al.* 2010). Additionally, species *A* may interact with both species *B* and *C* but depends strongly on *B* and only weakly on *C*. Intuitively, a management intervention designed to indirectly modify the abundance of species *A* is more likely to succeed if the abundance of *B*, rather than *C*, is directly controlled. A complication of including the interaction weight when calculating the maximum matching, however, is that empirical interaction strengths are to some extent stochastic and depend on proximate factors such as sampling method and intensity (Gibson *et al.* 2011). We overcome this issue by calculating all maximal cardinality matchings and then ranking them by their matching weight. By following this approach, we effectively give priority to the species that participate in the pathways that potentially have the largest impact on the community while acknowledging the limitations associated with sampling and its potential restrictions (Jordano 2016).

Methods

We next applied the previously defined framework to ten paired pollination networks. Each network pair was composed of a community invaded by a plant and a community “free” of the invasive species. Four pairs were obtained from natural or semi-natural vegetation communities in the city of Bristol, UK (Lopezaraiza-Mikel *et al.* 2007). These networks are comprised of 19–87 species (mean 55), and non-invaded plots were obtained by experimentally removing all the flowers of the invasive species *Impatiens grandiflora*. The other six pairs were obtained from lower diversity Mediterranean shrublands

171 in Cap de Creus National Park, Spain (Bartomeus *et al.* 2008). These networks are comprised of 30–57
 172 species (mean 38); in contrast to the above, uninvaded communities were obtained from plots that had not
 173 yet been colonised by either of the invasive species *Carpobrotus affine acinaciformis* or *Opuntia stricta*.
 174 Further details about the empirical networks can be found in Supporting Information S3.

175 We then specified the structure of all networks using pollinator visitation frequency, which has been
 176 shown to be an appropriate surrogate for interspecific effects in pollination networks (Vázquez, Morris
 177 & Jordano 2005; Bascompte, Jordano & Olesen 2006). To further examine whether this decision would
 178 influence our results, we also evaluated the effect of using pollinator efficiency or pollinator importance as
 179 alternative measures in a different data set that lacked invasive species (Ne'Eman *et al.* 2010; Ballantyne,
 180 Baldock & Willmer 2015), and we found quantitatively similar results for all three options (Supporting
 181 Information S4). Because our approach depends on the network topology, we also evaluated the robustness
 182 of our results to the undersampling of interactions. Specifically, we calculated n_D and species relative
 183 importance for 500 random subsamples of each empirical network in which the weakest links were more
 184 likely to be removed. Our sensitivity analysis indicated that, even in the absence of complete sampling, a
 185 control-theoretic approach can still be applied (Supporting Information S5).

Manageability

186 We began by quantifying the manageability of each network. To do so, we calculated the networks'
 187 maximum matching and determined the minimum proportion of species n_D that need external input
 188 signals to fully control the species abundances in the community. Note that because all maximum
 189 matchings have the same matching size, it is only necessary to calculate one of them. To simplify the
 190 analysis, if a network had more than one component (two species are in different components if there
 191 exists no path between them and are hence independent of each other in terms of network control) we
 192 only considered the largest. Smaller components were present in eleven out of the twenty networks and
 193 were typically composed of just one plant and one pollinator. Their removal represented an average loss
 194 of 4.7% of the species and 2.7% of the interactions.

Weighting & directing links

195 As we noted earlier, the maximum-matching approach requires a directed network in which a link from
 196 species i to species j indicates that the abundance of j can be affected by the abundance of i . This implies
 197 that we need first to identify a directionality for the links between species that is consistent with the
 198 dynamics of the community (Figure 2). In some ecological networks, establishing the directionality can
 199 appear relatively straightforward, for example when links represent biomass transfer or energy flow (Isbell

200 & Loreau 2013). Interspecific effects in pollination networks, however, are not strictly directed since the
 201 benefit is mutual between interacting species. Nevertheless, the relative extent to which a given pair
 202 of interacting species affect each other can be quantified by the magnitude of the mutual dependence
 203 between them (Bascompte *et al.* 2006). The dependence of plant i on pollinator j , d_{ij} , is the proportion
 204 of the visits from pollinator j compared to all pollinator visits to plant i . Likewise, the dependence of
 205 pollinator j on plant i , d_{ji} , is the proportion of the visits by pollinator j to plant i compared to all visits
 206 of pollinator j . Using dependences generates a weighted bipartite network in which all interacting pairs
 207 are connected by two directed links (Figure 2b).

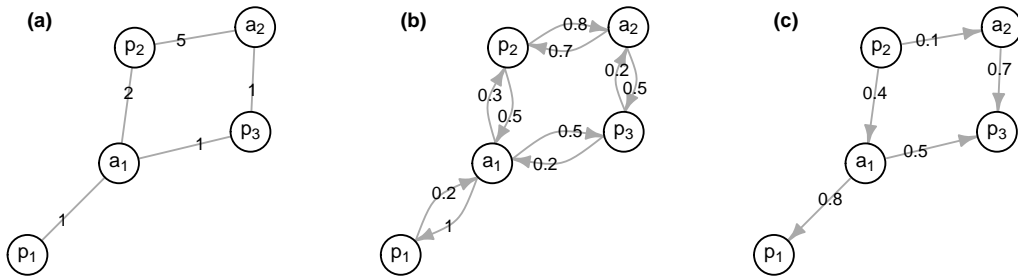


Figure 2: **Different ways to depict quantitative mutualistic networks.** (a) Pollination networks are frequently described by the observed number of visits between each plant and animal species. (b) Based on that visitation data, the mutual dependences between interacting species are calculated directly based on the relative visitation frequencies. (c) The relative differences of these dependences—the interaction asymmetry—then provide a means to estimate the dominant direction of the interspecific effects.

208 Given the respective dependences, the extent to which species i affects species j relative to the extent to
 209 which j affects i can be summarised by the interaction asymmetry (Bascompte *et al.* 2006) given by

$$a(i, j) = a(j, i) = \frac{|d_{ij} - d_{ji}|}{\max(d_{ij}, d_{ji})}.$$

210 Previous research has shown that mutual dependences are often highly asymmetric in natural communities
 211 (Bascompte *et al.* 2006); in other words, if a plant species is largely dependent on a pollinator species,
 212 then that pollinator tends to depend rather weakly on the plant (or vice versa). We therefore simplified
 213 the network so that interacting species are connected by only one directed link when mutual dependences
 214 are asymmetric (Figure 2c). This simplification, while maintaining ecological realism, is advantageous
 215 for several reasons. First, it is consistent with previous advances in structural controllability; second, it
 216 prevents the singular case in which the network could be perfectly matched rendering $D = 1$ as well
 217 as problems related to the introduction of artificial control cycles (Ruths & Ruths 2014); and third it
 218 significantly reduces the computational resources necessary for the application of our approach (Supporting
 219 Information S6). Moreover, we found that changing to unidirectional interactions based on the direction
 220 of asymmetry does not alter the relative n_D of different networks (Table S3).

221 To find a maximum matching in a network with interaction directions and weights determined by the

asymmetry, we adopted a strategy based on an alternative bipartite representation of the directed network with two levels that indicate the outgoing and incoming links to each node (Supporting Information S1). Once we had this alternative representation we used the maximum bipartite matching algorithm implemented in the `max_bipartite_match` function of `igraph` 1.0.1 (Csardi & Nepusz 2006) on each network.

Statistical analysis

We also wanted to test whether invasion status or other predictors had an impact on the observed values of n_D . We therefore used a set of generalised linear models (with binomial error structure) to investigate the effect of invasion status while also including covariates related to species richness, since one might naively expect to see a negative relationship between richness and manageability (Menge 1995). These covariates included the total number of species, plant richness, pollinators richness, the ratio of plant to pollinator richness, the link density (connectance), and the study site (as a two-level factor).

We next explored whether real networks differ in their architecture from random ones in a concerted way that affects manageability. Previous research indicates a direct link between a network's degree distribution and the number of nodes necessary to fully control it (Liu *et al.* 2011), but the strength and applicability of this relationship have not been tested for in weighted ecological networks. We therefore compared the driver-node density n_D of the empirical networks to networks generated by a null model that maintained each species' strength (its total sum of visits) while allowing their degrees (its number of interactions) to vary. Beyond network structure, the dependence asymmetry plays a fundamental role in determining the direction of control in each two-species interaction and therefore has the potential to influence the network n_D results above. We therefore performed an additional randomisation in which we kept the structure of each network constant but randomised the direction of the interaction asymmetries. That is, we first calculated the observed asymmetries for each community and then shuffled the direction of the link between each pair of species.

Additional details about the statistical models and the randomisations can be found in Supporting Information S7.

Relative importance

Our second key question was related to how species differ in their ability to drive the population dynamics of the community. To quantify this importance, we computed all maximal cardinality matchings in each network. We then calculated the frequency with which each species i was a driver (f_D) or a superior node (f_S) in the set of matchings that had a matching weight greater or equal to 0.8 times the

weight of the maximum matching. We selected this threshold as it provided a high agreement between networks quantified by visitation and pollination efficiency as well as between our weighting/directionality assumptions; however, the choice of this threshold had a negligible impact on any results (Supporting Information S8). Details about the computational procedure to find all maximal cardinality matchings of a network can be found in Supporting Information S1 and Figure S2.

Statistical analysis

We then examined whether any species-level structural properties could predict our metrics of species importance—the frequency with which a species was a driver or a superior node (f_D and f_S , respectively). We used a set of generalised linear mixed-effects models (with binomial error structure) with the relative frequencies as the response variables. As predictors in this model, we included measures of centrality (degree and eigen-centrality), which have been found to be strong predictors of importance in a coextinction context (Memmott, Waser & Price 2004); a measure related to network robustness (contribution to nestedness), as nestedness has been proposed as one of the key properties that promote stability in mutualistic networks (Saavedra *et al.* 2011); a measure of strength of association (visitation strength, the sum of visits a species receives or performs) and a measure of strength of dependence (species strength, the sum of dependences of all species on the focal species), as their distribution determines the extent of interspecific effects (Bascompte *et al.* 2006). In addition, we also included guild (plant or pollinator) and whether the species is invasive or not as categorical fixed effects. Lastly, we allowed for variation between different communities by including the network identity as a random effect (Bates *et al.* 2015). Supplementary details about the statistical models can be found in Supporting Information S7.

Results

Manageability

All of the networks had a driver-node density n_D between 0.55 and 0.92 (mean 0.76; Figure 3a). In addition, we found that, when controlling for potential species richness effects, the n_D of invaded communities was smaller to those of non-invaded communities (Figure 3b). Nevertheless, of the various covariates we explored, the ratio of plants to pollinators showed the strongest relationship with n_D (Figure 3c; Table S5). Specifically as the proportion of pollinators increases and the ratio plant/pollinator approaches unity, n_D decreases (all our communities had more pollinators than plants). Other covariates—connectance (link density) and species richness—had negative, but comparatively less important, relationships with n_D .

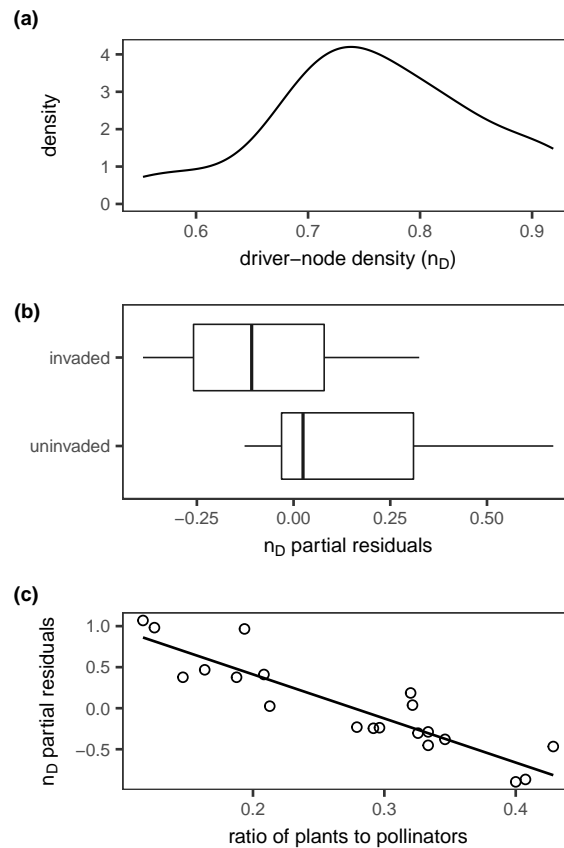


Figure 3: **Driver-node density.** (a) Histogram of the driver-node density (n_D) for the twenty networks. (b) Invaded communities have lower n_D than uninvaded communities even when controlling for factors related to species richness. The boxes cover the 25th–75th percentiles, the middle lines mark the median, and the maximum length of the whiskers is 1.5 times the interquartile range. (c) Out of the richness metrics, the ratio of plants to pollinators showed a strong, negative relationship with n_D . In both plots, partial residuals correspond to the partial working residuals of the invasion status in our generalised linear mixed model.

When exploring the effect of network structure itself, we observed that the driver-node density n_D of empirical networks was, in general, not significantly different to the manageability of network randomisations that maintained the degree of individual species (Figure 4). However, we found that the n_D of empirical networks was significantly larger than that of randomisations that maintained the network structure but that differed only in the direction of the asymmetries.

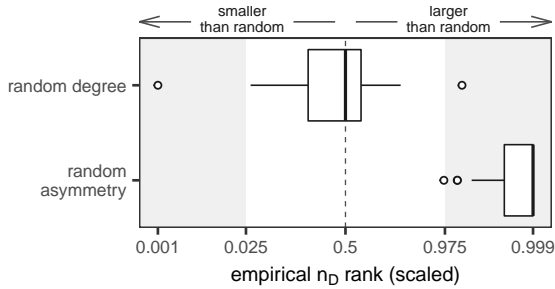


Figure 4: The driver-node density n_D of empirical networks compared to network randomisations. For each randomisation approach, we show the standardised rank of the empirical value compared to the set of randomisations. A scaled mean rank—akin to a p-value—less than 0.025 or greater than 0.975 (the areas shaded in light grey) suggests a significant difference between the empirical network and its randomisations. The empirical n_D is much larger than that of network randomisations in which the direction of asymmetries has been randomised. In contrast, the manageability of networks in which the species degrees were randomly shuffled were not significantly different. All boxes are as in Figure 3a.

Relative importance

Invasive species were classified as superior nodes and driver nodes in every single network they were present; that is, they always had the highest relative f_S and f_D (Figure 5a). The model results suggest that these differences between invasive and native species are not underpinned by any intrinsic property of the invasive species; instead, they are due to species properties that apply to invasive and native species alike (Table 1). Specifically, we found that a species is more likely to be classified as a superior node if it had a large species strength (the sum of the dependences of all other species on the species of interest). To a smaller extent, visitation strength (a species' sum of visits) and degree also had a positive relationship with f_S . In contrast, the relationships between species structural properties and f_D were less clear cut (Table 1). Both invasive species (which generally have a larger degree and high dependence strength) and pollinators (which generally have a smaller degree and low dependence strength) were classified as driver nodes in a large proportion of matchings.

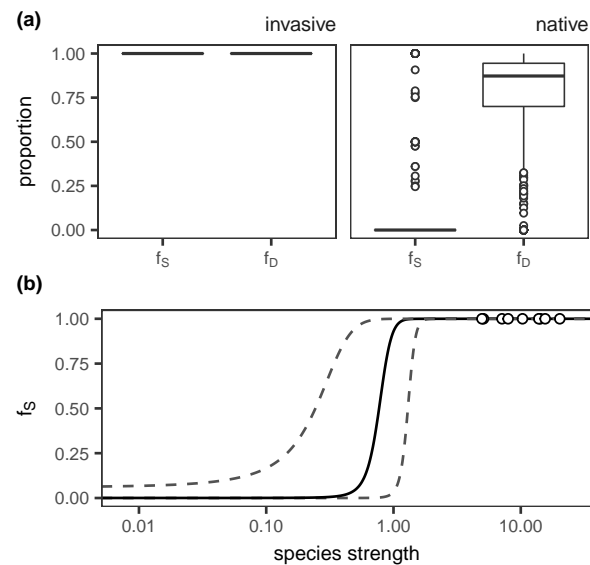


Figure 5: **Relationships between f_S and f_D and species structural properties.** (a) In all networks where they were present, invasive species were classified as superior (f_S) and driver (f_D) nodes in all possible control configurations. (b) Species strength (the sum of the dependences of other species on the species of interest) is the single most important factor explaining f_S . Visitation strength and degree also had an important albeit comparatively smaller effect (dashed lines correspond to \pm one standard deviation of these factors). Invasive species are depicted as circles.

Discussion

Contrary to our initial hypothesis, we found some evidence that invaded communities might be easier to manage than uninvaded ones from a control-theoretic perspective. Our results reveal, however, that this effect is comparatively small, and the structural differences among different networks are more strongly related to potential differences in our ability to alter the state of the community via external interventions. Despite the small effect of invasion status at the network level, we found that invasive mutualists occupy a particularly dominant role in their communities for two reasons. First, as species with a high f_S , changes on their abundance have the potential to propagate broadly through the community and, in turn, affect the abundances of many other species. Second, as species with a high f_D , they are also indispensable when it comes to fully controlling the plant-pollinator network. At a community level, we demonstrate that the manageability of mutualistic networks is strongly governed by the asymmetric nature of mutual dependences—which constitute the foundations of the structure and stability of mutualistic networks (Memmott *et al.* 2004; Vázquez & Aizen 2004; Bascompte *et al.* 2006; Astegiano *et al.* 2015). Moreover, these mutual dependences seem to be constrained by the effects of both the patterns of species richness at each trophic guild and a network's degree distribution (Melián & Bascompte 2002; Blüthgen *et al.* 2007). Indeed, the difference between the driver-node density (n_D) of our empirical networks and that of randomisations depended strongly on the null model's randomisation approach. While the empirical n_D was indistinguishable from that of networks with a random structure that maintained the degree of each

Table 1: **Factors explaining species importance.** Factor estimates correspond to the average over all models that accounted for 95% of the AIC evidence. Confidence intervals correspond to $\alpha = 0.05$.

	imp.	est.	C.I.
f_s			
(Intercept)	1.00	2.69	2.5
species strength	1.00	34.26	15
visitation strength	1.00	1.37	1.1
degree	0.90	4.12	5.5
contribution to nestedness	0.56	0.44	1.3
guild (pollinator)	0.48	0.72	2.6
eigen-centrality	0.25	0.00	0.19
invasive sp.	0.24	-6.23	3.2E+06
f_d			
(Intercept)	1.00	-0.19	0.83
guild (pollinator)	1.00	4.05	0.99
contribution to nestedness	1.00	1.41	0.62
degree	1.00	-5.31	2.5
species strength	1.00	4.65	2.6
visitation strength	1.00	3.07	2.7
eigen-centrality	0.71	0.72	1.5
invasive sp.	0.08	10.95	4.5E+06

species in the community, it was larger than that of randomisations in which the directed network was unchanged but where the observed patterns of dependence were broken.

Invasive species have been previously found to exacerbate the asymmetries in their communities (Aizen *et al.* 2008; Bartomeus *et al.* 2008; Henriksson *et al.* 2016). Although this might cause differences both at the community and the species level, we found that invasive plants are not inherently different to their native counterparts (Stouffer, Cirtwill & Bascompte 2014; Emer *et al.* 2016). Invasive plants, just like any other mutualist in our data set, tend to be classified as a superior node proportional to the degree to which their interaction partners are collectively more dependent on them than the other way around. Previous studies have found that supergeneralists, like invasive species, play a central role in their networks (Vilà *et al.* 2009; Palacio, Valderrama-Ardila & Kattan 2016). Our results take this one step further and indicate that dependence strength, rather than generalism or other metrics of centrality, is the factor that best explains the cascading effects a species could trigger on its community.

Because of the ability that our approach has to infer the magnitude of the effects that each species has on others in the community, it is tantalising to use it to select promising candidates for management interventions. To this end, the two indices we have used to characterise a species provide two complementary pieces of information. Our first index f_D —the frequency with which a species is classified as a driver node—provides an indication of the likelihood that a species forms part of the set of species that must be manipulated in order to control *all* species in the community. This driver-node concept has received considerable attention in the structural-control literature and indeed shows substantial potential to provide useful ecological insight. Nevertheless, we anticipate two caveats that hinder its direct utility

for management applications. First, unlike some other types of complex systems, fully controlling an ecological community is almost certainly out of reach for all but the simplest, due to either the number of required interventions or the practical difficulties of their implementation (Motter 2015). For instance, our results suggest that full control of the pollination networks would require direct interventions on anywhere from 40–90% of the species. Second, Ruths & Ruths (2014) established that driver nodes arise due to distinct mechanisms and therefore species with markedly different network metrics can act as driver nodes in their community (Supporting Information S2).

Our second index f_S , however, is directly related to the likelihood a species affects the abundance of another species in all of the control strategies considered. Importantly, this is irrespective of whether controlling the entire network is ultimately desired and/or feasible. In fact, because superior nodes are always at the beginning of a matched link, species with a high f_S are more likely to be the subjects of management interventions when controlling the abundances of a target set of species—as opposed to the entire network—is desired (Gao *et al.* 2014). An important advantage here is that the target set of species does not have to be the same set to which interventions are applied. For instance, despite inconsistent outcomes in practice (Suding, Gross & Houseman 2004; Rodewald *et al.* 2015; Smith *et al.* 2016), our results suggest that current restoration approaches that focus on direct eradication of invasive species might indeed be an effective way to modify ecosystem state. Nevertheless, our results also indicate that removals must be exercised with caution. Not only it is hard to predict the direction in which the system will change, but invaded communities also tend to be highly dependent on invaders and therefore acutely vulnerable to their eradication (Traveset *et al.* 2013; Albrecht *et al.* 2014).

Despite the apparent similarities, our approach is different to previous attempts to quantify species importance in a few key ways. Existing metrics usually harness species features, like centrality, position, co-extinction or uniqueness, to infer their effect on other species (Allesina & Bodini 2004; Jordán, Liu & Davis 2006; Jordán 2009; Lai, Liu & Jordan 2012). In contrast, our control-based approach tackles that question directly. Although they are relatively simple to calculate, classic species-level network metrics do not necessarily reveal the best set of species to manage (Eklöf, Tang & Allesina 2013; McDonald-Madden *et al.* 2016). Our approach, however, is not based on a single structural metric but instead acknowledges the existence of multiple management strategies. By allowing for the fact that some strategies are better than others depending on the context, control theory implicitly highlights that management decisions should not be based on a single technique. As such, ours and other flexible approaches that take a network-wide approach might prove more useful to guide ecosystem management (McDonald-Madden *et al.* 2016).

In this study, we illustrate how a control-theoretic approach can be employed in network ecology to evaluate the effect of invasions and other kinds of perturbations. We study the different ways a management

intervention can be structured and provide a starting point for the continued study of controllability in ecological contexts. Although our pollination-specific results might not be directly translatable to other ecological networks that do not have bipartite structures, the approach we propose is applicable wherever species abundances are influenced by their interactions, and exciting open questions lie ahead. How to design the precise “control signals” to reach a desired ecosystem state or conservation outcome? What are the implications of assuming fully nonlinear dynamics? How important it is to include several interaction types for our understanding of manageability and species importance? What are the implications for species coexistence? Which are the trade-offs between persistence at the species and the community level? Answering each of these questions might require its evaluation in different ecological systems, an explicit integration of control theory with numerical models of species densities (Cornelius *et al.* 2013; Gibson *et al.* 2016), and experimental tests on simple communities. Nevertheless, the potential rewards are encouraging from both an ecological and conservation perspective, where an integrated approach can shift the focus beyond the identification of ideal targets for intervention to the design of informed interventions that legitimately achieve restoration goals.

Appendix 1: Glossary

Driver node An unmatched node in a maximal cardinality matching or a maximum matching. From the control perspective, driver nodes are those to which external control signals must be applied in order to gain full control of the network.

Matched/unmatched link A link is referred to as *matched* if it is part of a matching, and *unmatched* otherwise.

Matched/unmatched node A node is referred to as *matched* if it is at the end of a matched link, and *unmatched* otherwise.

Matching A set of links in which no two of them share a common starting or ending node.

Matching size The number of matched links in a matching.

Matching weight The sum of the weights of all matched links in a matching.

Maximal cardinality matching A matching with the largest possible matching size. In un-weighted/binary networks, all maximal cardinality matchings are also maximum matchings.

Maximum matching A matching with the largest possible matching size *and* largest possible matching weight.

Superior node The node at the start of a matched link. From the control perspective, superior nodes make up the chains that propagate the control signals through the network.

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Author contributions

402 DBS conceived the idea; all authors contributed to the development of the theoretical framework. EFC
 403 performed all analysis. EFC and DBS wrote the manuscript. All authors contributed to its revision.

Data accessibility

404 All data used in this manuscript have already been published by Lopezaraiza-Mikel *et al.* (2007), Bartomeus
 405 *et al.* (2008), and Ballantyne *et al.* (2015). The reader should refer to the original sources to access the
 406 data.

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Quantifying the manageability of pollination networks in an invasion context

Supporting Information

E. Fernando Cagua, Kate L. Wootton, Daniel B. Stouffer

Contents

1	Finding a complex network's matchings	1
2	Control profiles	3
3	Properties of empirical networks	5
4	Visitation as a proxy for species interdependence	6
5	Sensitivity analysis	8
6	Chosing the direction of control	9
7	Statistical methods	12
7.1	<i>Manageability</i>	12
7.2	<i>Relative importance</i>	13
8	Matching's weight threshold	13
9	n_D models results	17
	References	17

1 Finding a complex network's matchings

Our approach to find the minumum number of driver nodes relies on finding maximum matchings and maximal cardinality matchings. We start with a directed network in which the direction of the link represents the direction of control (Figure S1a). We then construct an alternative representation of the directed network in which each node of the directed network is represented by two nodes that indicate their outgoing and incoming links respectively (Figure S1b). Finding a maximum matching in this alternative representation is equivalent to finding the largest possible set of edges in which one node on the left-hand side is connected to at most one node on the right-hand side. To find the maximum matching we use the push-relabel algorithm implemented in `max_bipartite_matching` in the R package `igraph` 1.0.1 (Csardi & Nepusz 2006). Once we have the matching (shown in the Figure S1b) it is then easy to identify the roles of each node in this representation: nodes on the left-hand side that are connected to a matched (purple) link are superior while those connected to a matched link on the right-hand side are matched. This information can then be mapped back to the original representation to identify the control paths and the driver nodes in the network (Figure S1c). Figure S1d–f illustrate this approach for a network with bidirectional links.

The algorithm implemented in `max_bipartite_matching`, however, is only able to find **one** of possibly many maximum matchings in a network. Though one maximum matching is enough to calculate n_D and

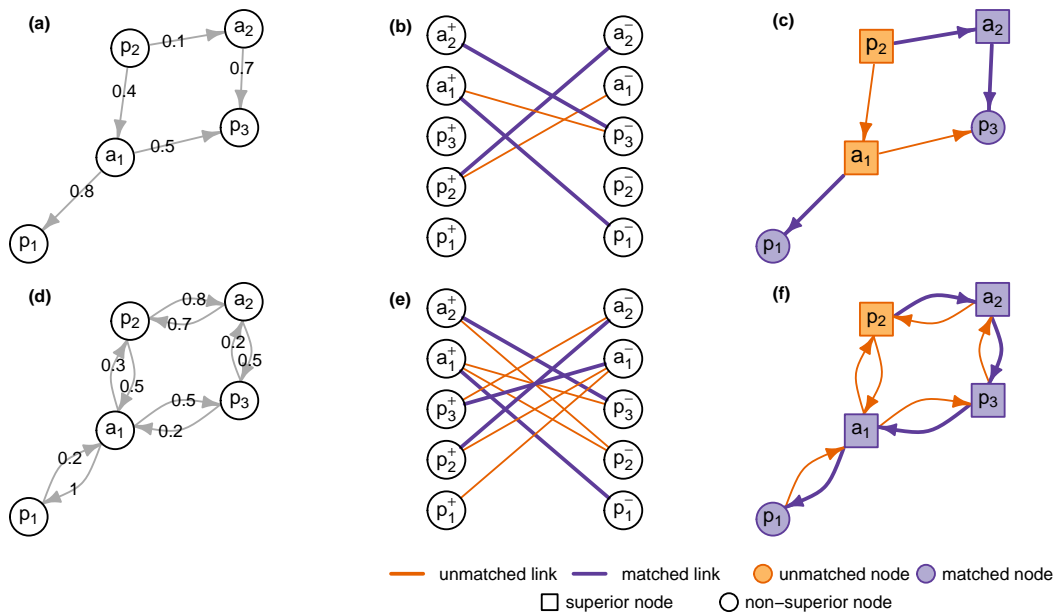


Figure S1: **Finding a maximum matching in a complex network.** (a & d) Directed networks that indicate the direction of control between species. (b & e) Alternative bipartite representations of the directed networks. (c & f) The matchings in the bipartite representation mapped back to the original network.

hence to provide indication of the manageability of a community, it is not sufficient to estimate the role of individual species. To do that, we need to calculate all possible maximum matchings (or, equivalently, all maximal cardinality matchings in weighted networks like ours). To do this, we again start from the alternative bipartite representation in Figure S1b and assign an identity to each of the links in the network (shown as numbers in Figure S2a). We will call this bipartite representation P . We then construct the line graph of the alternative bipartite representation $L(P)$ (Figure S2b). Each node in $L(P)$ represents a link in P and these are connected to each other only if and only if they share a common node in P . We then calculate H , the complement graph of $L(P)$ and identify all of its maximal cliques (Figure S2c). Here some extra definitions are necessary. First, H is a graph with the same nodes as $L(P)$ but that has a link between two nodes if and only if there is not a link in $L(P)$. Second, a clique is a subset of nodes such that all pairs of them are linked. Lastly, a maximal clique is a clique such that there are no cliques composed of more nodes (Gutin 2013). In this example, there are two maximal cliques: the one formed by 1, 3 and 5, and the one formed by 2, 3 and 5. The final step is then to map these cliques onto the original network to obtain all possible maximal cardinality matchings as shown in Figure 1 in the main text.

In the main text, we show all maximal cardinality matchings for a simple example network. To further illustrate our methodology here, we also show the approach for the smallest of our empirical networks, the uninvaded network at site 10 (Table S1; Figure S3). The largest component of this network is composed of 16 species of which two are non-invasive plants and the other 14 are pollinators. The one-to-one relationship between matched and superior nodes implies that in order to achieve full network controllability, most

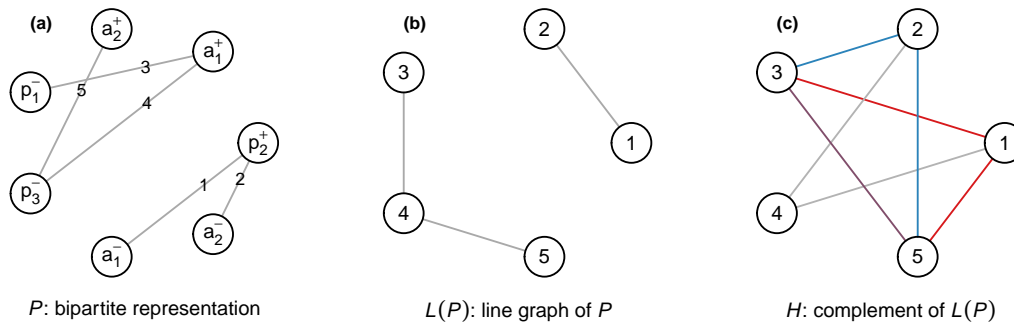


Figure S2: **Finding all possible maximal cardinality matchings.** (a) Alternative bipartite representation of the directed network in Figure S1a. (b) Line graph of the network in a. (c) Complement of the network in b. The two maximal cliques are shown in red and blue.

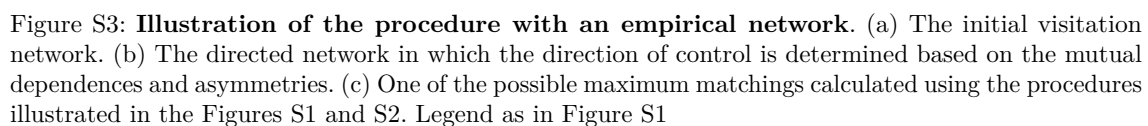
pollinators would be unmatched, and hence are classified as driver nodes that require external intervention. At the same time, both plants in the community, *Heracleum sphondylium* and *Rubus fruticosus*, and one of the pollinators, *Orthotylus/Lygocorus*, tend to be classified as superior nodes.

2 Control profiles

Ruths & Ruths (2014) proposed a heuristic-based method to provide insight into what might be required to control a network. The method is based on the idea that the reasons behind a node being classified as a driver node can be precisely identified, and that the relative contribution of these reasons can be used to characterise the control profile of the network. Specifically, nodes can be deemed to be driver nodes for any three reasons:

1. **Because it is a source node.** Source nodes are nodes that exclusively have outgoing links. Therefore, other nodes cannot control it and it must be externally controlled instead.
2. **Because of an external dilation.** Dilations occur whenever a control signal needs to branch out in order to reach all nodes in a network. One kind of dilation, which arises due to a surplus of sink nodes (those that only have incoming links) is called external dilation. This concept might be easier to understand by looking at Figure S3c. The source node a branches out into nine paths, but it can only control one of them. We say then that the sink nodes d to k become driver nodes because of an external dilation.
3. **Because of an internal dilation.** The remaining dilations (those that do not arise from a surplus of sink nodes) are called internal dilations. Node j in Figure S3c and the driver nodes in Figure S7 are examples of this category.

Mathematically, the number of driver nodes D is the sum of the number of source nodes, the number of external dilation points, and the number of internal dilation points, $D = N_s + N_e + N_i$. A network can



then be characterised by the relative proportion of the three kind of controls

$$\eta_s + \eta_e + \eta_i = 1,$$

where $\eta_s = N_s/D$, $\eta_e = N_e/D$, and $\eta_i = N_i/D$. These terms can be calculated with relative ease. D can be calculated using a maximum matching algorithm. N_s can be calculated by inspecting the network's degree distribution. $N_e = \max(0, N_t - N_s)$, where N_t is the number of sink nodes in the network. And we can solve for N_i once we have all other information.

Upon applying this framework to our networks with directions determined by asymmetry we, identify that they are all external dilation dominated (Figure S4). Ruths & Ruths (2014) explains that “external-dilation-dominated networks exhibited strong aspects of top-down control”. Because of the surplus of sink nodes, an external intervention that is applied to a source node will induce a correlated response among their subordinate species. For example, an increase in the abundance of *Heracleum sphondylium* (Figure S3) is likely to induce an increase in the abundance of the pollinators it interacts with. Therefore it can be expected that in order to fully control the network it is not sufficient to just apply interventions to the source nodes.

The control profile of our pollination networks provides additional justification for our decision to determine the importance of a species not only by its f_D but also with f_S . Many species that act like control sinks in our network will be classified as a driver node because they are necessary to *fully* control the dynamics of the community as opposed to playing a central role in influencing the abundance of other species in the community.

Using the Ruths & Ruths (2014) approach also highlights the importance of appropriately selecting the direction of control (see Section 6). A network with bidirectional links weighted by the mutual dependences would have zero source nodes and zero sink nodes. Therefore, the control profile of such a network would have been completely uninformative, as it would just highlight that the proportion of internal dilations is $\eta_i = 1$.

3 Properties of empirical networks

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## since toeplitz is already defined in the 'spam' namespace
```

The networks studied had species richness ranging between 19 and 87 (16–86 when considering only the largest component in each network). As shown by the network asymmetry AS (Blüthgen *et al.* 2007), the

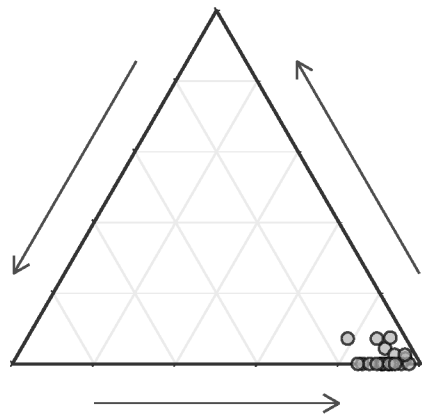


Figure S4: **Control profiles of the studied networks.** Following Ruths & Ruths (2014), profiles are shown in a ternary plot in which the corners correspond to points (1, 0, 0), (0, 1, 0), and (0, 0, 1) in the three-dimensional (η_s, η_e, η_i) space such that $\eta_s + \eta_e + \eta_i = 1$, and η_s, η_e , and $\eta_i > 0$.

networks had a low ratio of plants to pollinators overall. Furthermore, the networks had relatively low levels of nestedness (when measured using the quantitative version of the NODF index; Almeida-Neto & Ulrich 2011). Details for each network can be found in Table S1.

4 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 *et al.* 2005; Bascompte *et al.* 2006). Nevertheless visitation is not equivalent to pollen deposition and might be insufficient to reflect the dependences of plants on animals and vice versa (Alarcón 2010; King *et al.* 2013). We therefore investigated the effect of calculating the dependences using visitation or pollination effectiveness and importance—two metrics more proximate to plant reproductive success (Figure S5). We did this by comparing (i) the manageability of the community and (ii) the percentage of interactions that maintained the direction of dependence. To do this, we used data collected by Ballantyne *et al.* (2015) from a low diversity pollination community at a dry lowland heathland in Dorset, UK (50° 43.7'N 2° 07.2'W). First, 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 *et al.* 2013; Ballantyne *et al.* 2015). Second, visitation networks were constructed by counting the visits to flowers during Single Visit Depositions. Finally, pollinator importance networks were constructed as the product of pollinator efficiency and visit frequency.

At a network scale (Figure S5), the driver-node density n_D was consistent among the three weighting

Table S1: **Properties of the analysed plant-pollinator communities.** Invasive plants were *Carpobrotus affine acinaciformis* (car), *Opuntia stricta* (op), and *Impatiens grandulifera* (imp). All properties, with the exception of the networks' total species richness (R), correspond to the network's largest component. We show the number of species (n_s), the number of plants (n_p), the number of pollinators (n_a), the network connectance (c), the network asymmetry (AS), and the network nestedness (NODF index). British networks were assembled by Lopezaraiza-Mikel et al. (2007), Spanish were networks assembled by Bartomeus et al. (2008).

site	invader	R	n_s	n_p	n_a	c	AS	NODF	location
1	—	35	35	9	26	0.17	-0.49	8.68	Cap de Creus, Spain
1	car	57	57	10	47	0.17	-0.65	13.27	Cap de Creus, Spain
2	—	40	38	9	29	0.18	-0.53	12.66	Cap de Creus, Spain
2	car	38	38	11	27	0.21	-0.42	15.04	Cap de Creus, Spain
3	—	31	29	6	23	0.22	-0.59	14.30	Cap de Creus, Spain
3	op	33	28	6	22	0.24	-0.57	13.29	Cap de Creus, Spain
4	—	35	35	10	25	0.17	-0.43	12.43	Cap de Creus, Spain
4	car	57	57	14	43	0.14	-0.51	13.70	Cap de Creus, Spain
5	—	35	33	7	26	0.23	-0.58	13.05	Cap de Creus, Spain
5	op	32	32	8	24	0.19	-0.50	10.96	Cap de Creus, Spain
6	—	30	25	7	18	0.23	-0.44	9.77	Cap de Creus, Spain
6	op	37	37	9	28	0.17	-0.51	12.45	Cap de Creus, Spain
7	—	37	30	3	27	0.38	-0.80	24.86	Bristol, United Kingdom
7	imp	57	57	8	49	0.20	-0.72	14.36	Bristol, United Kingdom
8	—	48	43	3	40	0.36	-0.86	6.84	Bristol, United Kingdom
8	imp	87	83	13	70	0.12	-0.69	8.67	Bristol, United Kingdom
9	—	55	53	11	42	0.14	-0.58	13.77	Bristol, United Kingdom
9	imp	86	86	11	75	0.13	-0.74	13.40	Bristol, United Kingdom
10	—	19	16	2	14	0.57	-0.75	13.35	Bristol, United Kingdom
10	imp	54	49	5	44	0.26	-0.80	9.04	Bristol, United Kingdom

schemes (0.33 for deposition, 0.33 for the visitation, and 0.38 for the pollinator-importance network, respectively). The choice of weighting can also have an impact on at the species level. Therefore we calculated f_D and f_S (the frequency at which each species is classified as a driver or superior node, respectively, within the set of all possible maximal cardinality matchings in a network) and calculated its correlation among all three weighting schemes. Although visitation and deposition produce moderately different results, we found a very strong agreement between the order produced by visitation and importance (Table S2). Finally, we also investigated whether the asymmetry of mutual dependence, which defines the direction of control, was consistent among the three possible weighting schemes. We found again that the direction of the dominant dependence was maintained was consistent for 95% of the interactions weighted by visitation or importance, the two most appropriate metrics for pollinator and plant dependence (Table S2).

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

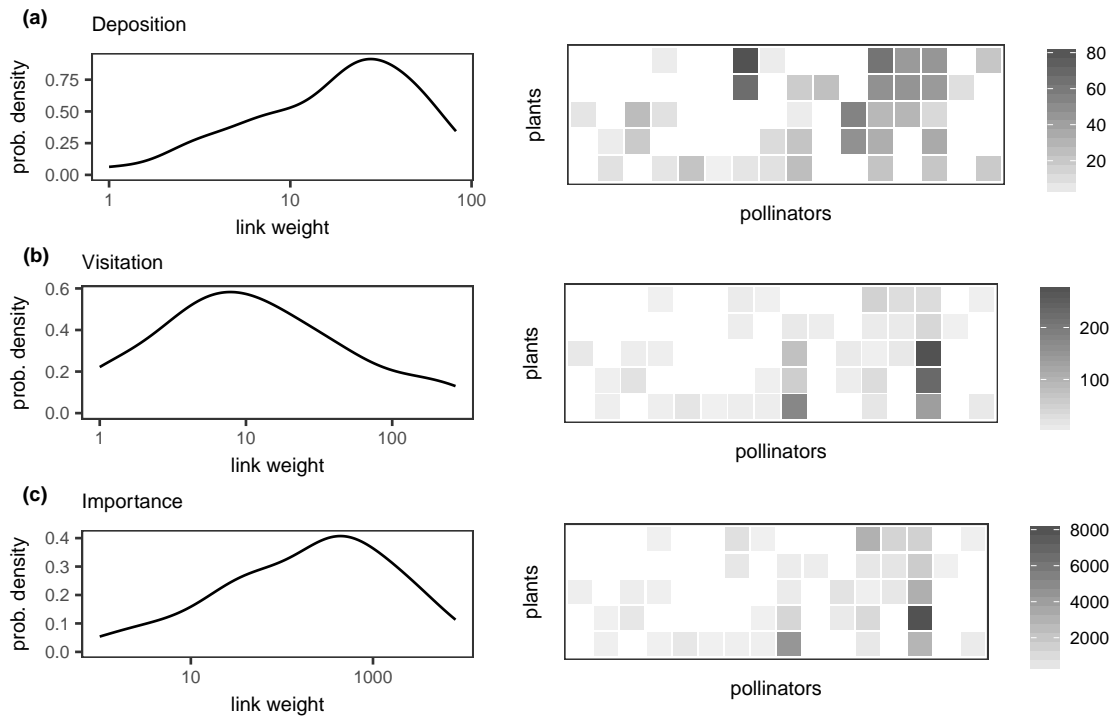


Figure S5: **Distribution of interaction weights for the pollen deposition, visitation and pollinator importance networks.** Note that the x axes in the density plots have been log-transformed.

Table S2: **Agreement among network weighting schemes.** Spearman correlation coefficients (with p-value) of species' f_D and the percentage of interactions that share the direction of dependence obtained using the three weighting schemes and an unweighted scheme.

	unweighted	deposition	importance	visitation
unweighted	-	0.93 (< 0.001)	0.85 (< 0.001)	0.85 (< 0.001)
deposition	87%	-	0.86 (< 0.001)	0.87 (< 0.001)
importance	77%	74%	-	1 (< 0.001)
visitation	82%	74%	95%	-

5 Sensitivity analysis

Our approach is fundamentally based on the network structure. Often, the majority of the interactions that make up this structure are weak; in our networks this means that most interactions are formed by a small number of observed pollination visits, and therefore those weak intercatons are less conspicuous in the field than strong ones. To strengthen the case of our approach, we therefore evaluated the robustness of our results to simulated sampling limitations.

To do so we removed a portion of the links, for each network, and calculated how three control metrics of the subsampled network compare to those of the full network. Specifically, we calculated the difference between the n_D of the subsampled and the full network, the Spearman correlation between the vectors f_D —which contain the frequency with which each species is classified as a driver species, and the Spearman

correlation between f_S —which contain the frequency with which each species is classified as a superior node. We removed links from the full network with a probability inversely proportional to the interaction weight, and varied the portion of links removed between 50% and 95% at 5% increments. We repeated the procedure ten times for each removed level and each network to obtain a total sample size of $n = 2000$.

Overall, the results of the sensitivity analysis indicate that our approach might still be useful for management even in the absence of complete sampling. Specifically, as the proportion of sampled interaction decreased, the variability of n_D increased, but was overall very similar to that obtained when using all available interactions (Figure S6a). Similarly, the correlation between the relative frequency with which species are classified as a driver (f_D) or as a superior node (f_S) was highly correlated even for *extreme* levels of undersampling (Figure S6b). For instance, we found that with a sampling level of 50%, the mean Spearman correlation coefficient was 0.66 for f_D and 0.76 for f_S . Finally, the results suggest that the relative ranking of species is better conserved in f_S than for f_D throughout all subsampling levels.

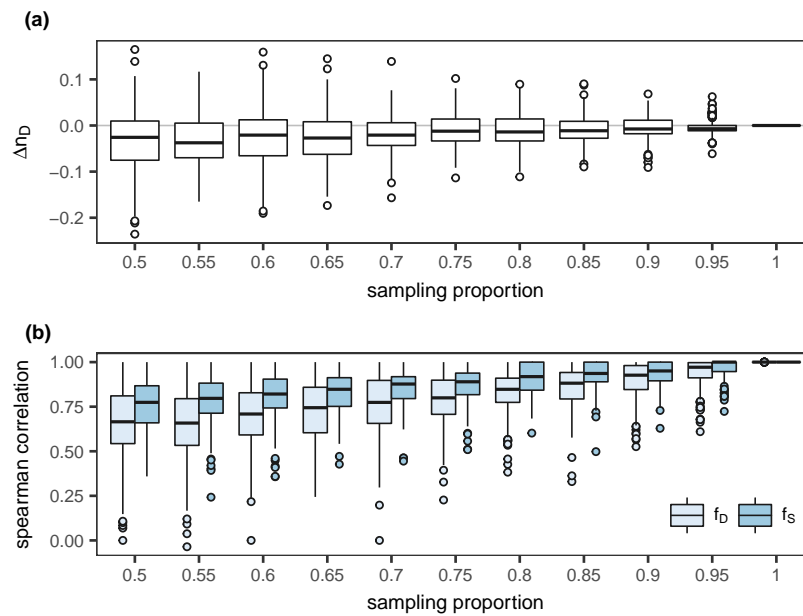


Figure S6: **Sensitivity to subsampling.** (a) The difference between the n_D of the subsampled and the full networks. (b) The spearman correlation of the relative importance of species between the subsampled and the full networks.

6 Chosing the direction of control

Our decision to adopt the direction of asymmetries as the direction of control is coherent with ecological processes and also confers several advantages. First, it is consistent with previous studies, which facilitates

the comparability between our findings and those in other systems explored using structural controllability. Second, it reduces the number of control cycles in the network—which require special treatment in our approach. Third, the reduced number of links facilitates the computation of all possible maximum matchings.

For illustration, we show all maximal cardinality matchings for an example network in which links are weighted based on the mutual dependences and not asymmetries (Figure S7). We note, however, that using mutual dependences, or indeed any set up that can lead to bidirectional links, is problematic for a couple of reasons. First, having two links between interacting species and using our maximum matching approach to calculate the control configurations, can result in matchings that include cycle inducing links (Figure S8). Strictly speaking these configurations are maximal cardinality matchings in the alternative bipartite configuration (Figure S1e) but not in the directed network (Figure S1f). While bidirectional links are the norm when using mutual dependences, they only appear in the asymmetry-weighted networks whenever the mutual dependences between two species are strictly symmetric. In this special case, we include two links weighted with 0.5 to reflect the fact that the species affect each other to the same extent.

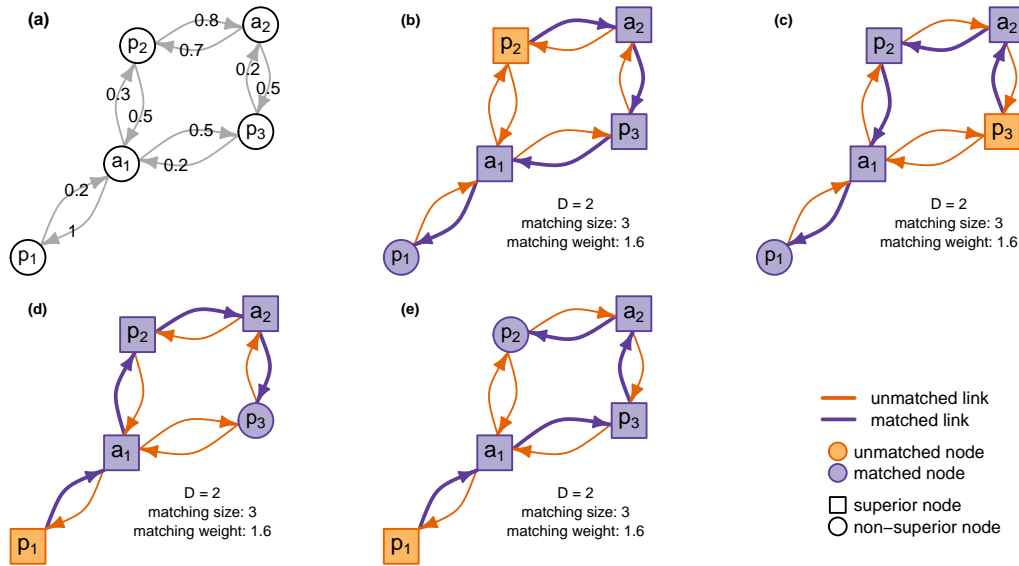


Figure S7: **Matchings of a simple network with bidirectional links.** (a) A network with bidirectional links. (b-e) All possible control configurations.

We consider two ways to tackle this limitation. The first, is to calculate the matching(s) as usual and then, before calculating f_S and f_D , filter out the cycle containing matchings (Figure S8). In the special case that the network has no maximal cardinality matchings that correspond to feasible control configurations because they all include cycles, we reduce the size of the cliques we enumerate in H (Figure S2) and repeat. Instead of calculating the matching(s) for the network with bidirectional cycles, in the second approach, we calculate the matching(s) of 2^n unidirectional versions of the network, where n is the number

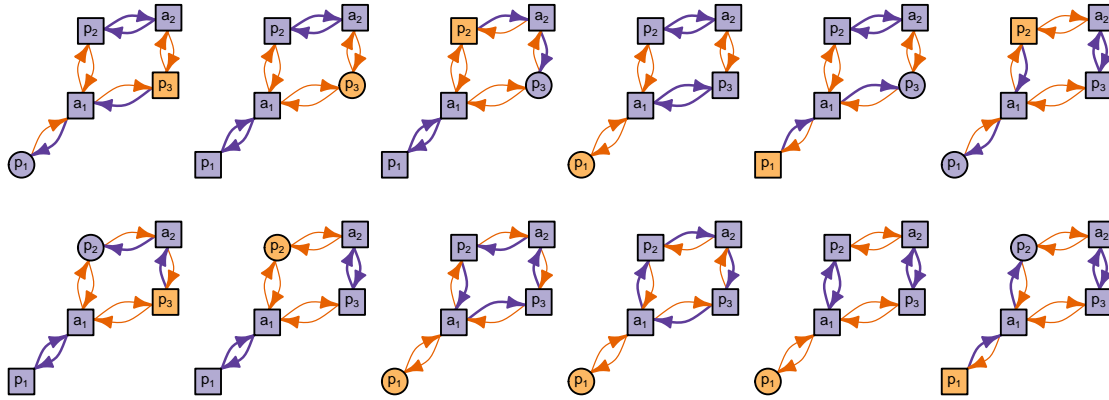


Figure S8: **Cycles in a bidirectional network.** Our approach finds twelve configurations for Figure S7a that are matchings in the alternative bipartite representation but not in the directed network.

of bidirectional cycles in the network (Figure S9). We then average the results of these unidirectional networks to find the overall f_S and f_D for a given species.

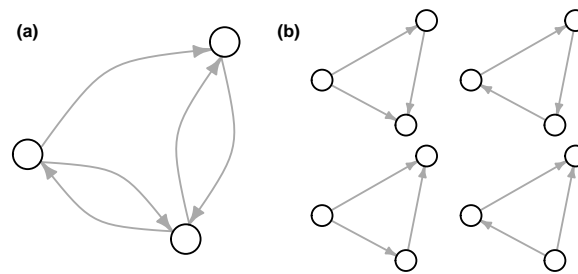


Figure S9: **Dealing with cycles.** The network on the left, which has $n = 2$ bidirectional cycles, can be decomposed into 2^n unidirectional networks.

The number of maximal cardinality matchings increases disproportionately fast with the number of links in a network. For instance, our example network in Figure 1, which is composed of unidirectional links weighted by the asymmetry, has two different maximal cardinality matchings. In contrast, the equivalent network with bidirectional links has 16 different maximal cardinality matchings (Figure S7 and S8). To further illustrate the implications of this growth, some of our empirical networks had approximately ten thousand different maximal cardinality matchings using asymmetries but one hundred million when using mutual dependences. Consequently, the computational cost of either filtering matchings with cycles or calculating the matchings for 2^n networks surpassed the capabilities of our available computational resources and rendered us unable to calculate all possible maximal cardinality matchings when using mutual dependences in most of our bidirectional networks. Nevertheless, as most of our networks weighted by asymmetry had between zero and four cycles, we successfully used the second approach explained in the previous paragraph to calculate the all maximal cardinality matchings for these networks.

We highlight that although the direction of control might affect the f_S and f_D , it doesn't strongly affect

the network’s relative driver-node density n_D . We reached this conclusion by calculating the n_D obtained assuming that (a) the direction of control is governed by the asymmetry, (b) bidirectional dependences, (c) that plants depend on pollinators, or that (d) pollinators depend on plants. Although the n_D values were quantitatively different between the approaches (Figure S10), the Spearman correlation among these four options suggested a very high agreement (Table S3).

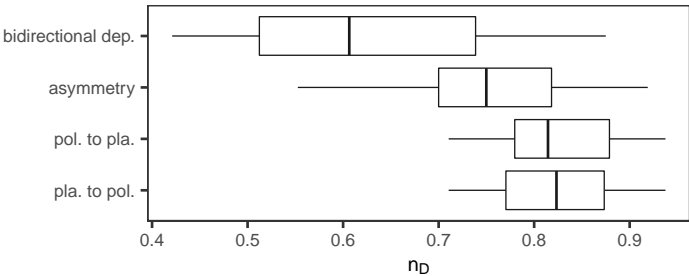


Figure S10: **Absolute differences among assumptions on the direction of control.**

Table S3: **Agreement among assumptions on the direction of control.** Spearman correlation coefficients of the driver-nodes density n_D four different assumptions of the direction of control..

	pol. to pla.	asymmetry	bidirectional dep.
pla. to pol.	1	0.97	0.96
pol. to pla.		0.98	0.96
asymmetry			0.98

7 Statistical methods

7.1 Manageability

7.1.1 Genrealised linear models for n_D

Candidate models were compared using AICc and the relative importance of the explanatory variables was evaluated using the sum of Akaike weights over candidate models that accounted for 95% of the evidence (Burnham & Anderson 2003; Bates *et al.* 2015; Bartoń 2016). Coefficient estimates were averaged following Buckland *et al.* (1997) while confidence intervals were calculated following Lukacs *et al.* (2010). Only models that accounted for 95% of the evidence weight were considered to quantify the relative importance of the fixed effects.

7.1.2 Network randomisations

Randomisations that maintained the degree of the visitation networks were generated using the quasiswap-count algorithm and the function `commsim` in `vegan` 2.3-3 (Oksanen *et al.* 2016). After generating the

randomised networks, we then calculated the mutual dependences and interaction asymmetries of each and determined n_D using our maximum-matching framework. Finally, we calculated the average rank (akin to a p-value) of n_D for each empirical network compared to the corresponding values of each set of 999 randomisations (Veech 2012).

Similar as in the previous null model, to evaluate the effect of the direction of the asymmetries, we calculated the average rank of the empirical n_D when compared to that of the randomisations.

7.2 Relative importance

7.2.1 Genrealised mixed effects models for f_S and f_D

To facilitate comparison among the continuous variables, we scaled them so that they all had a mean of zero and a standard deviation of one. Although the importance of plants and pollinators or invasive and non-invasive species could respond differently to our structural metrics, our data set did not contain enough variation to include the corresponding interactions terms for these latter two predictors. All network metrics were calculated using the R package bipartite 2.06 (Dormann *et al.* 2008). Candidate models and estimates were assessed using the same procedure as in the models for n_D .

8 Matching's weight threshold

We use the frequency with which a species is classified as a driver node f_D and the frequency with which a species is classified as a superior node f_S in a set of accepted maximal cardinality matchings to infer their relative importance. Maximal cardinality matchings were accepted if the matching weight was over a certain threshold. This threshold was defined as a proportion of the maximum matching's weight. Here we evaluate the impact that a particular choice of this threshold has on both f_D and f_S . The number of accepted maximal cardinality matchings increased rapidly as the threshold at which they are accepted decreases. Nevertheless, this number stabilises below approximately 0.6-0.7 (Figure S11).

We then examined how species relative importance changes with the chosen threshold. We observed, that regardless of the matching weight's threshold, species tended to be superior nodes in all or none of the matchings, which equates to f_S values of one or zero, and the differences between important and unimportant species were maintained (Figure S12). In contrast, species' f_D reached intermediate levels of importance and showed higher variability across thresholds (Figure S13). We note here that we were unable to compute all the maximal cardinality matchings for one of our networks (uninvaded community

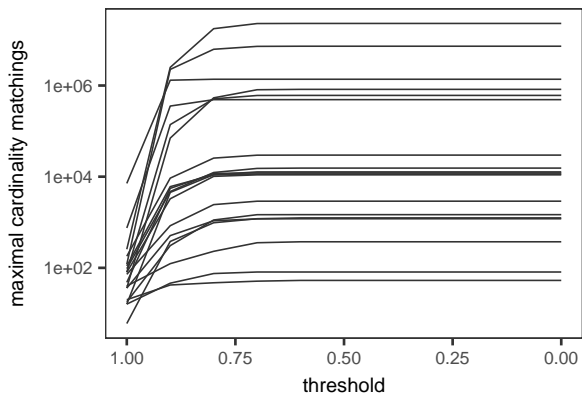


Figure S11: **Number of maximal cardinality matchings as a function of the weight threshold.** Each line corresponds to one network.

in site 8). This is because, we estimated the number of matchings to be more than one billion, and this surpassed our available computational resources.

Finally, we examined the agreement across thresholds by calculating the Spearman correlation matrix of species' f_S and f_D for each network. The mean of those matrices is shown in Table S4. Among all thresholds, we found a very high agreement for f_S , and high to very high for f_D . With the exception of using a threshold of 1 (only maximum matchings are accepted), the choice of the threshold has limited impact on the relative importance of species. For convenience, we use an intermediate level of 0.8. Nevertheless, the differences are marginal and any threshold ≤ 0.9 is likely to produce very similar results.

Table S4: **Spearman correlation coefficient among different matching weight thresholds.** The upper triangle shows values for f_D and the lower triangle shows values for f_S

	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1
0	—	1	1	1	1	1	1	0.995	0.947	0.83	0.402
0.1	1	—	1	1	1	1	1	0.995	0.947	0.83	0.402
0.2	1	1	—	1	1	1	1	0.995	0.947	0.83	0.402
0.3	1	1	1	—	1	1	1	0.995	0.947	0.83	0.402
0.4	1	1	1	1	—	1	1	0.995	0.947	0.83	0.402
0.5	1	1	1	1	1	—	1	0.995	0.947	0.83	0.402
0.6	1	1	1	1	1	1	—	0.995	0.947	0.832	0.404
0.7	1	1	1	1	1	1	1	—	0.953	0.845	0.426
0.8	1	1	1	1	1	1	1	1	—	0.903	0.493
0.9	0.994	0.994	0.994	0.994	0.994	0.994	0.994	0.994	0.995	—	0.642
1	0.982	0.982	0.982	0.982	0.982	0.982	0.982	0.982	0.983	0.987	—

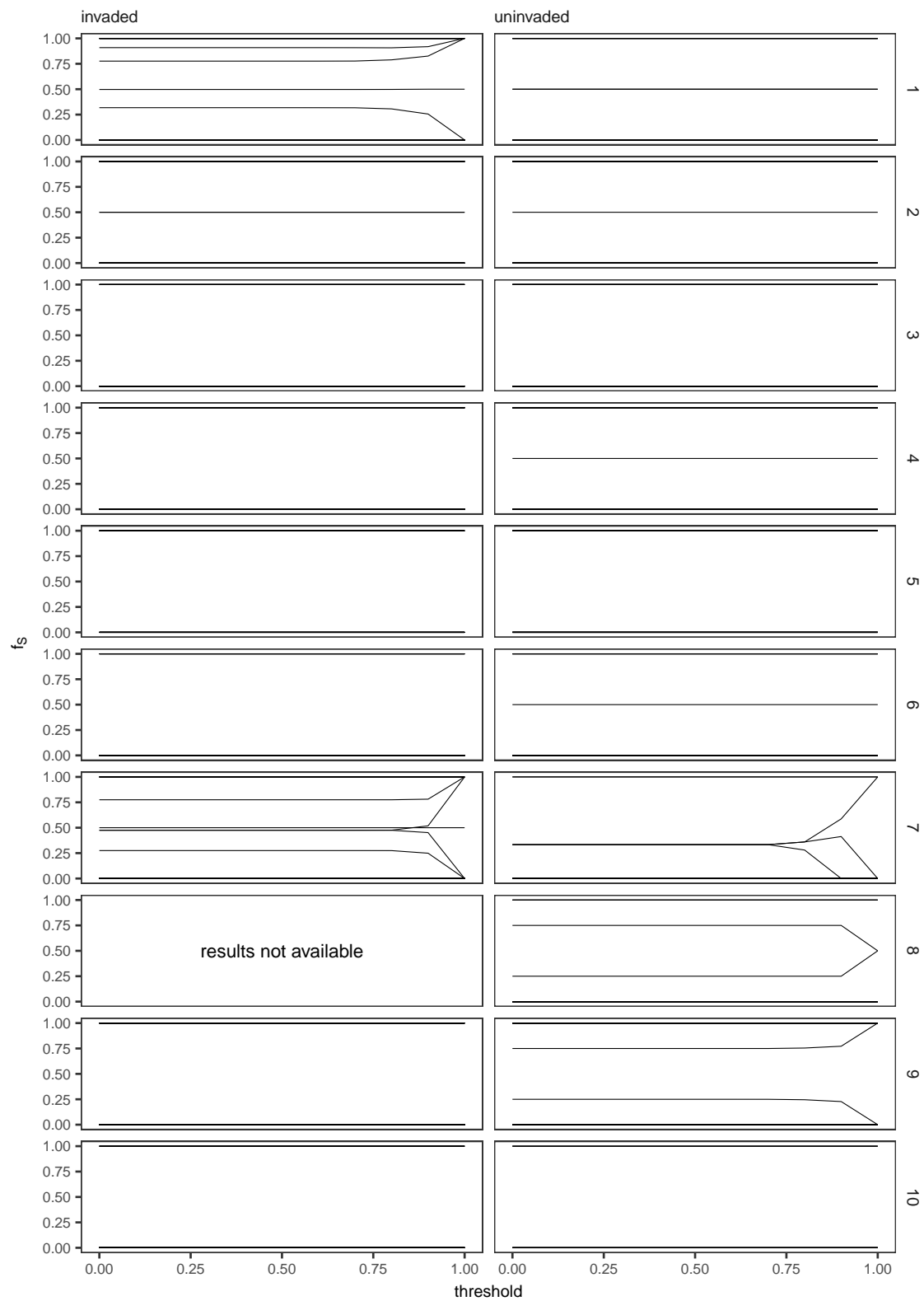


Figure S12: Relative frequency with which a species was classified as a superior node (f_s) as a function of the matching weight threshold. Rows correspond to network pairs.

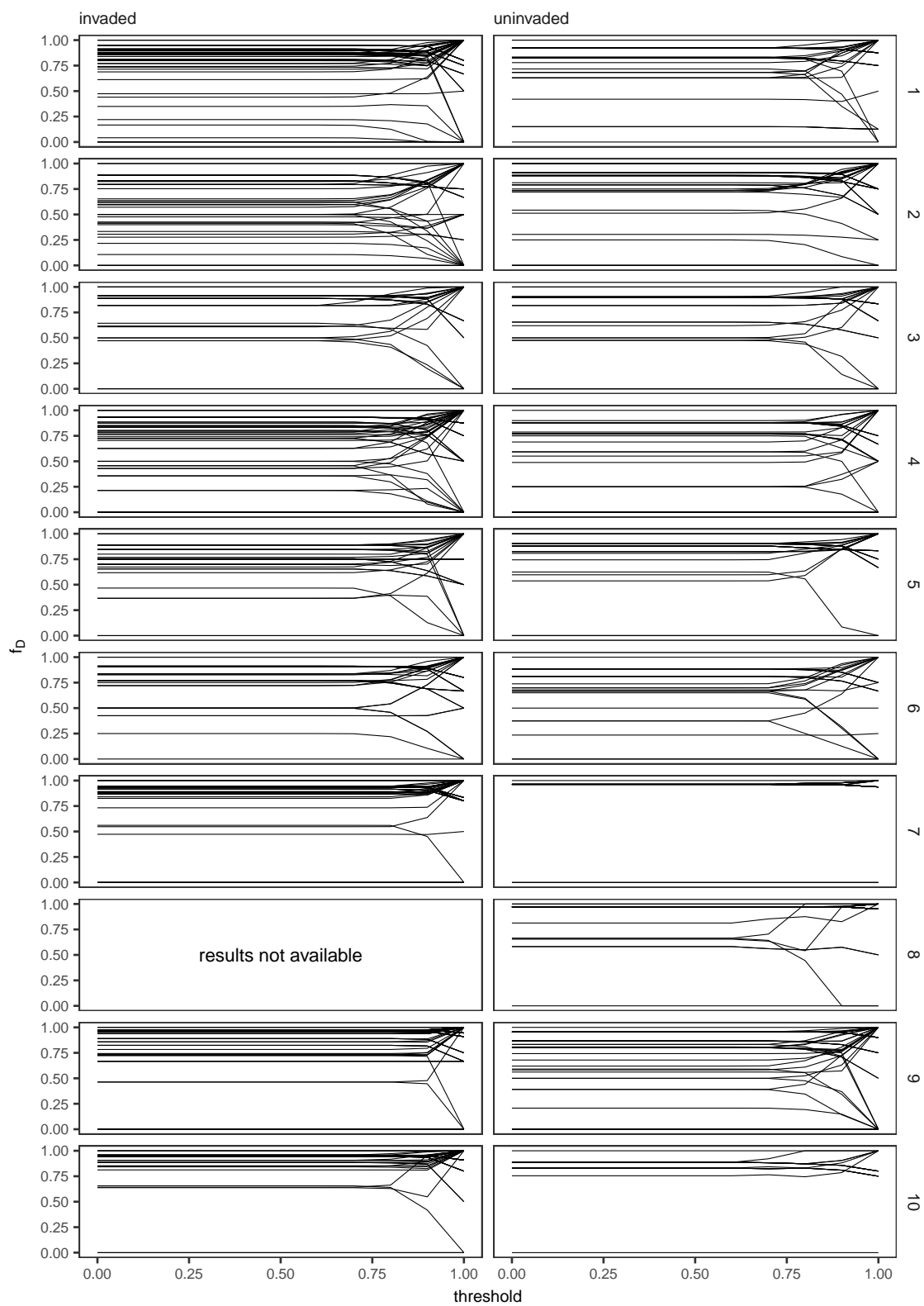


Figure S13: Relative frequency with which a species was classified as a driver node (f_D) as a function of the matching weight threshold. Rows correspond to network pairs.

9 n_D models results

Table S5: **Coefficients of the n_D models.** Estimates are averaged over the models that accounted for 95% of the evidence weight.

	est.	imp.	C.I.
(Intercept)	3.75	1.00	3.1
ratio plant/pollinator	-5.96	1.00	3.6
spp. richness	-0.01	0.66	0.024
connectance	-2.54	0.48	7.9
invasion status	-0.04	0.32	0.21
study site	0.08	0.30	0.33

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