The manageability of pollination networks in an invasion context

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- **Running title:** Manageability of pollination networks.
- **Keywords:** Network control, ecological networks, species importance, driver species, food webs, mutualism, management interventions, food web, interaction asymmetry, mutual dependence
- **Article type:** Letter.
- **Number of words:** 183 abstract; approx. 5460 main text.
- **Number of references:** 72
- **Number of displays:** 5 figures; 1 table.
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- **Authorship:** DBS conceived the idea; EFC, DBS and KLW contributed to the development of the theoretical framework. EFC performed all analysis. EFC and DBS wrote the manuscript.
- **Data accessibility:** All data used in this manuscript have already been published by Lopezaraiza-Mikel *et al.* (2007), Bartomeus *et al.* (2008), and Ballantyne *et al.* (2015). The reader should refer to the original sources to access the data.

Abstract

It is generally unknown how the disruptions caused by perturbations like biotic invasions affect our ability to manage ecological communities. Here, we capitalise on recent advances in control theory to assess the "manageability" of ten pairs of uninvaded and invaded plant-pollinator communities. We found that the manageability of the studied networks is strongly determined by the relative richness of plants and pollinators, which in turns constraint the species' degree distribution. Furthermore, we characterise species potential to be candidates for management interventions using metrics that explore the entire space of control strategies. Specifically, we use 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. Remarkably, we found that invasive plants have a dominant position in every community in which they were found and that this dominance is underpinned by the high asymmetry in the dependence of their interaction partners. Our results highlight the advantages of using a control theoretic framework to answer ecological questions, at the same time it provides insight into the design of informed management interventions.

Introduction

Complex systems are chahave bracterised by relationships in which the whole is often greater than the sum of its parts (Jørgensen *et al.* 1998; Levin 1999; Montoya *et al.* 2006). Within community ecology, a complex systems approach has led to the development of a variety of analytical and simulation tools with which to understand, for example, the role of species when embedded in an intricate network of interactions (Pascual & Dunne 2005; Bascompte & Stouffer 2009; Stouffer *et al.* 2012). The inherent complexity of nature, however, has regularly hindered—or at least greatly complicated—our ability to find management solutions to the 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 (Solé & Montoya 2001; Green *et al.* 2005). Ideally, such a framework needs to be able 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. This method, widely used in engineering to determine and supervise the behaviour of dynamical systems (Motter 2015), is well equipped to deal with the many feedbacks present in ecological communities (Liu 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 *et al.* 2011; Cornelius *et al.* 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. Furthermore, 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 provide an indication of which species are most relevant from a structural and dynamic perspective.

This information is valuable not only from an ecological perspective, but it might be also relevant to address 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 either alter the state of invaded ecosystem 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 (Baxter *et al.* 2004; Tylianakis *et al.* 2008; Ehrenfeld 2010). Understanding how the differences in network structure before and after the invasion impact our ability to manage the communities double challenge, it is a critical first step towards a fully informed recovery. Despite the apparent overlap, a control-theoretic perspective has not been adopted in an invasion context. This is perhaps because of a lack of appropriate methodological tools that can account for the observed variation in the strength of interspecific effects that are characteristic of ecological networks (Liu *et al.* 2011; Isbell & Loreau 2013).

To bridge this gap, we outline an approach to apply theory on the control of complex systems in an ecological context and implement them using empirical data. Specifically, we use a set of ten pairs of uninvaded and invaded plant-pollinator communities to investigate the link between invasion, network structure and ecological management. While doing so, we focus on two particular questions. First, grounded on the difficulties usually involved with invasive species eradication and ecosystem restoration (Woodford *et al.* 2016), we ask whether invaded networks have lower levels of "manageability" than their uninvaded counterparts; that is, whether they require a greater proportion of species to be managed to achieve the same level of control. Second, we ask whether some species are more important than others at driving the population dynamics of the community and which factors determine this importance. We focus on these two particular applications for a variety of reasons. First, biotic invasions are known to produce tractable changes in the structure of ecological networks, and these changes can be particularly pronounced in mutualistic networks between plants and pollinators where biotic invasions have been shown to modify the strength of species interactions and the degree of network nestedness and connectivity (Olesen *et al.* 2002; Aizen *et al.* 2008; Bartomeus *et al.* 2008; Vilà *et al.* 2009; Traveset *et al.* 2013). Second, although species are involved in multiple types of interactions, plant-pollinator networks provide an ideal framework to answer these questions. On the one hand, community networks that quantify relative levels of interaction are readily available. On the other, the bipartite nature of pollination networks makes it possible to simplify assumptions of how these interactions translate into interspecific effects.

Methods

Theoretical framework

Disregarding practical considerations, any network could hypothetically be fully controlled if we control the state of every single node individually. At the core of control theory of complex networks, however, rests the idea that the state of a node depends on the state of the nodes it interacts with, and the particular form of this dependence is determined both by the dynamic relationship among interacting nodes as well as the structure of the links in the network. This principle can, therefore, be harnessed to find a subset of *driver nodes* to which to apply external input signals which then drive the state of every other node in the network to a desired configuration.

Conveniently, in a network with linear dynamics, the information necessary to determine the minimum number of driver nodes D is fully contained in the network structure (Kalman 1963; Liu *et al.* 2011; Motter 2015). We, therefore, start here from the assumption that an ecological network can, at least near equilibrium points, be described by $\frac{dx}{dt} = Ax + Bu(t)$, where the change over time of its state ($\frac{dx}{dt}$) depends on its current state x (for example the species' populations), an external time-varying input $u(t)$, and the matrices A and B, which encapsulate information about the network structure and how the species respond to the external input, respectively. Even though linearity might be a strong assumption, it has been shown that fundamental insight about the control of complex systems can be gained without a detailed knowledge of the nonlinear dynamics and the system parameters (Liu 2016), an important step towards ultimately understanding the controllability of systems with nonlinear dynamics (Liu *et al.* 2011). This means that structural controllability can be applied to a wide range of readily available network representations of ecological communities to provide a strong indication of our ability to control them. Moreover, we show here how quantitative data about species interactions can help us move past some of the limitations of structural controllability by better approximating the role of interspecific dynamical relationships without being overly dependent on the specific choices of how these dynamics are modelled or characterised.

Manageability

The number of driver nodes D can provide a structural indication of how difficult its 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, can be seen as a metric of the extent to which network structure can be harnessed for network control. For instance, while a hypothetical "network" in which species do not interact but instead function independently from each other would require direct interventions in every single species to achieve full control, a linear food chain would require just one species to be directly controlled to harness cascading effects through the trophic levels that compose it. 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 *maximal cardinality* if the number of matched links (also referred to as the *matching size*) is the largest possible. A maximal cardinality matching is then called a *maximum matching* if the sum of the weights of the matched links (also referred to as *matching weight*) is again the largest possible (West 2001). Note that this implies that for unweighted binary networks, all maximal cardinality matchings are also maximum matchings.

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

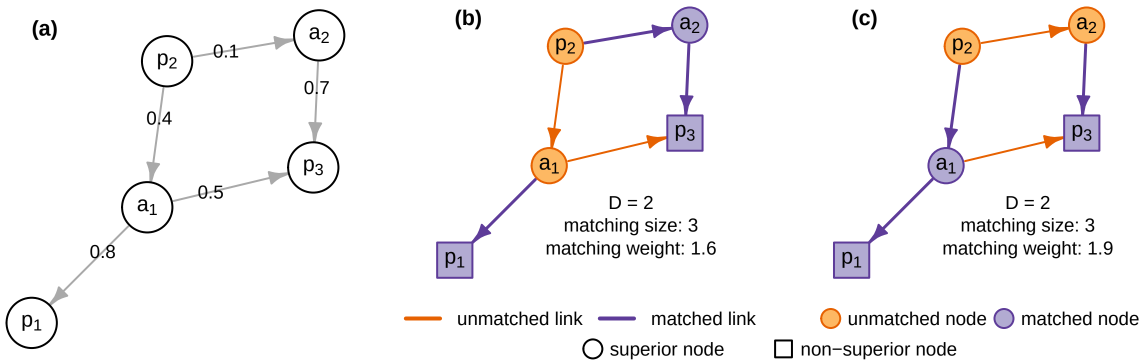

Figure 1: **Matchings of a simple network**. (a) We start with a network in which the direction of the links indicates the potential direction of control; for example a link from a_1 to p_1 indicates that the state of p_1 is influenced by the state of a_1. (b & c) This network has two maximal cardinality 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 the Supporting Information S1.

Note that this framework requires a directed network in which the direction of the links corresponds to the direction of control. In the "Empirical application" section below, we explain our approach to determining the link direction in pollination networks.

Relative importance

While calculating n_D provides an indication of the manageability of an ecological community, it does not provide information about the identity of the species that compose the set of driver nodes. Ecologically, these distinctions are acutely relevant because management and conservation resources are limited, and therefore ecological interventions should ideally be focused on the set of species that might provide the largest impact. Maximum matchings in a network are often not unique, and each different maximum matching indicates a unique path that can potentially be used to control the network. We harness this property and use a network's complete set of multiple maximum matchings to characterise a 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. However, the profile of our networks indicates that a large proportion of driver nodes are so, because of external interventions are 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 still 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 superior nodes 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 because it has been shown that the weights can reveal significant ecological patterns and processes that might be undetectable in unweighted networks (Scotti *et al.* 2007; Tylianakis *et al.* 2007; Vázquez *et al.* 2007; Kaiser-Bunbury *et al.* 2010). For example, a species A interacts 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 a 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 circumvent this issue by calculating all maximal cardinality matchings and subsequently 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).

Empirical application

We now describe the application of 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 *Impatients grandulifera*. The other six pairs were obtained from lower diversity Mediterranean shrublands in Cap de Creus National Park, Spain (Bartomeus *et al.* 2008). These networks are comprised of 30–57 species (mean 38); in contrast to the above, uninvaded communities were obtained from plots that had not yet been colonised by either of the invasive species *Carpobrotus affine acinaciformis* or *Opuntia stricta*. Further details about the empirical networks can be found in the Supporting Information S3.

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

Manageability

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

Weighting & directing links

Recall that the aforementioned maximum-matching approach requires a directed network in which a link between species i and j pointing to species j indicates that the abundance of j can be affected by the abundance of i. This implies that we need first to identify a directionality for the links between species that is consistent with the dynamics of the community (Figure 2). In some ecological networks, establishing the directionality can appear relatively straightforward, for example when links represent biomass transfer or energy flow (Isbell & Loreau 2013). Interspecific effects in pollination networks, however, are not strictly directed since the benefit is mutual between interacting species. Nevertheless, the relative extent to which a given pair of interacting species affect each other can be quantified by the magnitude of the mutual dependence between them (Bascompte *et al.* 2006). The dependence of plant i on pollinator j, d_{ij}, is the proportion of the visits coming from pollinator j compared to all pollinator visits to plant i. Likewise, the dependence of pollinator j on plant i, d_{ji}, is the proportion of the visits by pollinator j to plant i and all visits of pollinator j. As the dependences are not necessarily symmetric, their use generates a weighted bipartite network in which all interacting pairs are connected by two directed links (Figure 2b).

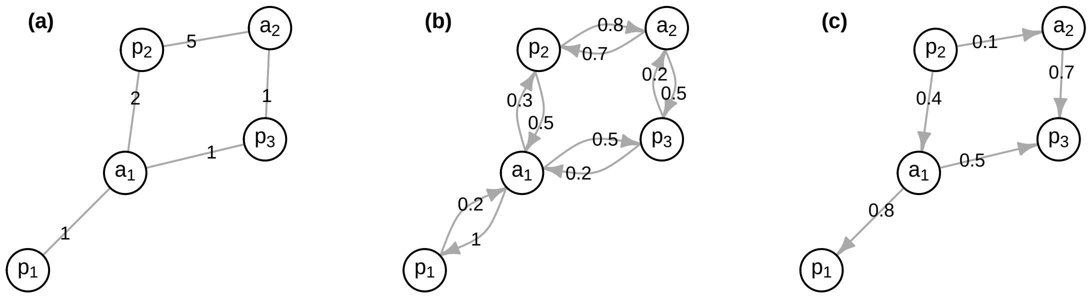

Figure 2: **Different ways to depict quantitative mutualistic networks**. (a) Pollination networks are frequently described by the observed number of visits between each plant and animal species. (b) Based on that visitation data, the mutual dependences between interacting species are calculated directly 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.

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

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

Previous research has shown that mutual dependences are often highly asymmetric in natural communities (Bascompte *et al.* 2006); in other words, if a plant species is largely dependent on a pollinator species, then that pollinator tends to depend rather weakly on the plant (or vice versa). We, therefore, simplified the network so that interacting species are connected by only one directed link when mutual dependences are asymmetric (Figure 2c). This simplification, while maintaining ecological realism, is advantageous for several reasons. First, it is consistent with previous advances in structural controllability; second, it avoids complications related to the introduction of artificial control cycles; and third it significantly reduces the computational resources necessary for the application of our approach (Supporting Information S6). Furthermore, we show that changing to unidirectional interactions determined by the observed direction of asymmetry, as a surrogate of bidirectional mutual dependences does not alter the relative n_D of different networks (Table S3).

To find a maximum matching, we adopted a strategy based on an alternative bipartite representation of the directed network in which the two levels indicate the outgoing and incoming links to each node

(Supporting Information S1). Once we had this alternative representation, then, on each network, we used the maximum bipartite matching algorithm implemented in the `max_bipartite_match` function of igraph 1.0.1 (Csardi & Nepusz 2006).

Statistical analysis

Although understanding the variability of manageability across ecological networks is a useful result in itself, we also wanted to test whether invasion status had an impact on the observed n_D. We, therefore, used a set of generalised linear models (with binomial error structure) to investigate the effect of invasion status while also controlling for factors 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). 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).

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. Randomisations were generated using 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 one of each set of 999 randomisations (Veech 2012).

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. Similar to the other null models, we calculated the average rank of the empirical n_D when compared to that of the randomisations.

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 is deemed to be 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 S7).

Details about the computational procedure to find all maximum 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 can predict our metrics of species importance—the frequency to 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 *et al.* 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); and two measures of strength of association and dependence (visitation and dependence strength, this is the sum of visits a species receives or performs, and the sum of dependences of all species on the focal species, respectively), as their distribution determines the extent of interspecific effects (Bascompte *et al.* 2006). To facilitate comparison among the continuous variables we scaled so that they all had a mean of zero and a standard deviation of one. In addition, we also included guild (plant or pollinator), and whether the species is invasive or not, as categorical fixed effects. 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). Lastly, we allowed for variation between different communities by including the network identity as a random effect (Bates *et al.* 2015). Candidate models and estimates were assessed using the same procedure as in the n_D models.

Results

Manageability

All of the networks studied had a driver node density n_D between 0.55 and 0.92 (mean 0.76. 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 3a; Table S5). Nevertheless, of the various covariates we explored, the ratio of plant to pollinator showed the strongest relationship with n_D (Table S4). Specifically, we found that as the proportion of pollinators increases and the ratio plant/pollinator balances, n_D decreases (all our communities had more pollinators than plants). Other coovariates—connectance (link density) and species richness—had a negative and comparatively less important relationship with n_D.

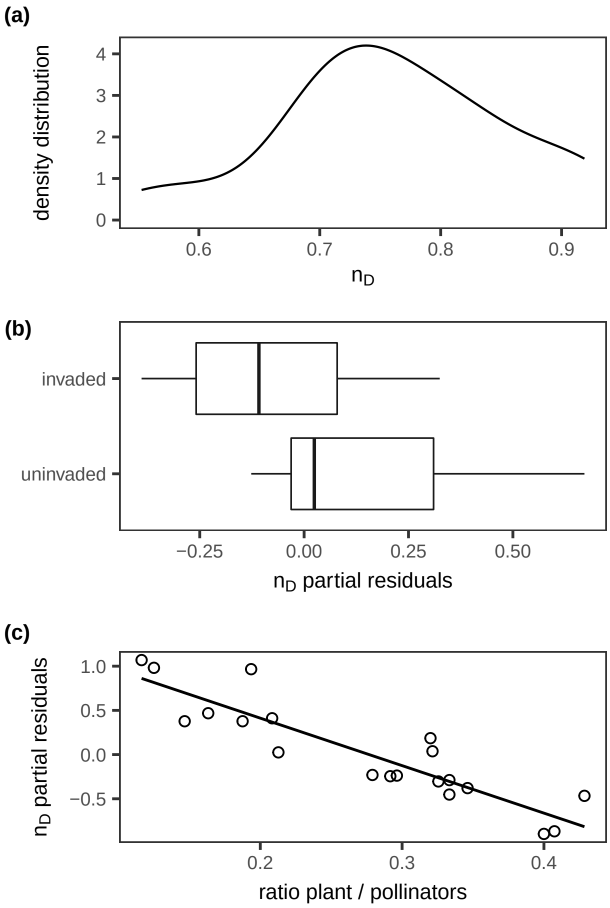

Figure 3: **Driver node density**. (a) Density distribution of the proportion of driver nodes (n_D) for the twenty studied networks. (b) Invaded communities have lower proportion of n_D than uninvaded communities even when controlling for factors related to species richness. The boxes cover the 25th–75th percentiles, the middle lines mark the median, and the maximum length of the whiskers is 1.5 times the interquartile range. All points outside this range are indicated by the circles. (c) Out of the richness metrics, the ratio of plants to pollinators showed an important relationship with n_D. In both plots, 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 to that of randomisations that maintained the network structure but that differed only on the direction of the asymmetries.

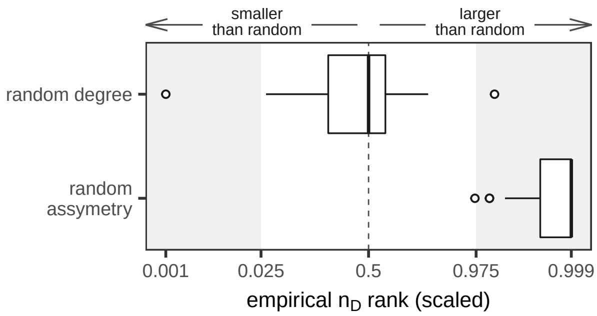

Figure 4: **The driver node density n_D of empirical networks compared to network randomisations**. For each randomisation approach, we show the standarised rank of the empirical value compared to the set of randomisations. A scaled mean rank—akin to a p-value— less than 0.025 or greater than 0.975 (the areas shaded in light grey) suggests a significant difference between the empirical network and its randomisations. The empirical n_D is much smaller 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 this differences among invasive and native species are underpinned, not by any intrinsic property of the invasive species but instead, by 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 other species on the species of interest). To a smaller extent, visitation strength (its sum of visits) and the species degree also had a positive relationship with f_S. In contrast, the relationships between species structural properties and f_D were more convoluted (Table 1). Both invasive species (which for example tend to have a large degree, and high dependence strength) and pollinators (which generally have a smaller degree and dependence strength) were classified as driver nodes in a large proportion of the considered matchings.

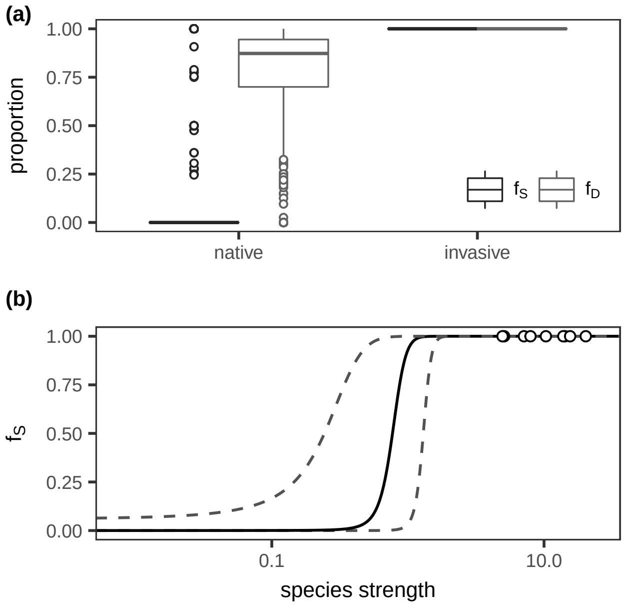

Figure 5: **Relatiosnships between f_S and f_D and species' structural properties**. (a) In all networks were they were present, invasive species were classified as superior (f_S) and driver (f_D) nodes in all possible control configurations. (b) Species strength (the sum of the dependences of other 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 ± one standard deviation on 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. Our results reveal, however, that this effect is comparatively small and the structural differences among different networks are more importantly related to potential differences in our ability to alter the state of the community. Despite the small effect of invasion status at a network level, we found that invasive mutualists occupy a particularly dominant role in their communities. Not only changes on their abundance have the potential to propagate broadly trough the community and in turn, affect the abundances of many other species, but they are also indispensable to fully control 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; Lever *et al.* 2014; Astegiano *et al.* 2015). Moreover, these mutual dependences seem to be importantly constrained by the concerted effects of both, the patterns of species richness at each trophic guild, and the species' 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 evaluated null model. While the empirical n_D was indistinguishable from that of networks with a random structure that maintained the degree or strength of each species in the community, it was much larger than that of randomisations in which the directed

Table 1: **Factors determining species importance**. Factor estimates correspond to the average over all models that accounted for 95% of the AIC evidence.

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

Confidence intervals correspond to an alpha risk of 0.05.

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 *et al.* 2014). Invasive plants, just like any other mutualist in our data set, tend to be classified as a superior node with a frequency (f_S) 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 super-generalists, like invasive species, play a central role in their networks (Vilà *et al.* 2009; Palacio *et al.* 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. The two indices we employed to characterise a species provide two complementary pieces of information. Our first index, the frequency with which a species is classified as a driver node (f_D) provides an indication of the likelihood the species is part of the set of species that need to be intervened in order to control of *all* species in the community. The 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 other types of complex systems, fully controlling an ecological community is realistically out of reach for all but the most simple ones; either because of the number of required interventions or the difficulties of their implementation (Motter 2015). For instance, our results suggest that full control of the pollination network would require direct interventions on 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 be driver nodes in their community (Supporting information S2).

Our second index f_S is, however, directly related to the likelihood a species has to affect the abundance of another species in all of the considered control strategies. Importantly, this is irrespective of whether controlling the entire network is desired/feasible or not. In fact, because superior nodes are invariantly at the beginning of a matching 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—and not the entire network—is desired (Gao *et al.* 2014). An important advantage is that the target set of species does not has to be the same set to which interventions are applied. For instance, despite inconsistent outcomes in practice (Suding *et al.* 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 also, invaded communities tend to be highly dependent on invaders and therefore acutely vulnerable to their eradication (Traveset *et al.* 2013; Albrecht *et al.* 2014).

Although f_S, in particular, is promising for identifying species priorities, our approach is different to previous attempts to quantify species importance. Existing metrics usually harness species features like centrality, position, co-extinction or uniqueness, to infer their effect on other species (Allesina & Bodini 2004; Jordán *et al.* 2006; Jordán 2009; Lai *et al.* 2012). Contrastingly, our control-based approach, by definition, tackles that question directly. Although relatively simple to calculate, it has been shown that classic species-level network metrics do not necessarily reveal the best set of species to manage (Eklöf *et al.* 2013; McDonald-Madden *et al.* 2016). Our approach, however, is not based on a single structural metric but acknowledges the existence of multiple management strategies; some more optimal than others in specific contexts. Our, and other flexible approaches that take a network-wide approach might prove more useful to guide ecosystem management if we want to go beyond using network metrics to minimise topological species loss (McDonald-Madden *et al.* 2016).

Despite its conceptual advantages, our approach still relies on knowledge of the network of interaction between species. We do not argue that management decisions should be based on a single technique. Nevertheless, our results and previous basic research show that as long as the proportion of sampled links is enough to provide indication of the actual degree distribution (and in turn the species dependences), n_D, f_S and f_D can still provide a simple, straightforward, and theoretically-informed indication of the degree to which the community is self-regulated and therefore how difficult it might be to modify its state in one way or another using some of the species that integrate it (Supporting Information S5; Nepusz & Vicsek 2012).

In this study, we illustrate how a control-theoretic approach can be adopted in network ecology to evaluate the effect of invasions and another kind of perturbations. Although, because of the degree constraints imposed by bipartite networks, our pollination specific results might not be relevant to other ecological systems, the approach we propose is applicable wherever species abundances are influenced by their interactions. 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 linear species dynamics? How important 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 these questions might require its evaluation on 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 rewards are encouraging. Not only from a purely ecological perspective, but also from a conservation perspective, where an integrated approach can shift our focus beyond the identification of ideal targets for intervention to design 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 refered to as *matched* if it is part of a matching, and *unmatched* otherwise.

Matched/unmatched node A node is refered 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 particular matching.

Maximal cardinality matching A matching with the largest possible matching size. In unweighted networks, all maximal cardinality matchings are also maximum matchings.

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

The node at the start of a matched link. From the control perspective, superior nodes make up the chain(s) that propagate the control signal(s) through the network.

Acknowledgments

The authors thank Dr. Takeuki Uno for the insight provided to find the set of all maximum matching algorithms, and Jason Tylianakis, Bernat Bramon, Warwick Allen, Matthew Hutchinson, and Marilia Gaiarsa for feedback and valuable discussions. EFC acknowledges the support from the University of Canterbury Doctoral Scholarship, the University of Canterbury Meadow Mushrooms Postgraduate Scholarship, a New Zealand International Doctoral Research Scholarship, and a travel grant from the European Space Agency. DBS acknowledges the support of a Marsden Fast-Start grant and a Rutherford Discovery Fellowship, administered by the Royal Society of New Zealand.

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