Biotic invasions reduce the manageability of mutualistic networks

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

Center of Integrative Ecology, School of Biological Sciences, University of Canterbury

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Network manageability in the context of species invasion

Introduction

Complex systems, such as ecological communities, are characterised by non-linear relationships in which the whole is greater than the sum of its parts . This complex systems approach has led to the development of a rich suite of analytical and simulation tools with which to understand the role of species when embedded in an intricate network of interactions. However, in contrast to other types of complex systems like neural, intra-organizational, or trust neworks, ecological networks do not have a hierarchical or distributed structure but rather tend to be closed systems in which resources recirculate. As such, ecosystems contain multiple feedbacks that allow them to self-regulate and, therefore, function relatively independent from external stimulation. This complex propertes have hindered, or at least complicated, our ability to find management solutions to the many problems ecological communities face. A framework that allow us to explain, predict, and manage ecological communities, particularly when they are faced with perturbations, need be able to account for their complex structure, and the dynamics that determine the state of each species—and the community as a whole. Control theory might be a good candidate framework as it is designed to deal with determining and supervising the behavior of a dynamical system and is well equiped to deal with the many feedbacks presents in ecological communities.

Research stemming from control theory has established a strong link between the structure of complex networks and their controlability, and that, in principle, it is possible to alter a ecological community's composition by modifying the abundances of only a few species (Liu, Slotine, and Barabási 2011; Cornelius, Kath, and Motter 2013). Based on this work, it has been suggested that the degree distribution of ecological networks makes them inherently difficult to control (Liu, Slotine, and Barabási 2011; Ruths and Ruths

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2014). This theoretical result is in agreement with many examples in which the management and restoration of ecological communities is more challenging than aticipated. For instance, biotic invasions, as a major drivers of global change, can induce dramatic changes on the patterns of interactions that determine the structure of ecological networks (Baxter et al. 2004; Tylianakis et al. 2008; Ehrenfeld 2010). The difficulties of returning invaded communities to a predisturbance state can be evidenced by the limited amount of success of restoration projects (Suding, Gross, and Houseman 2004; Rodewald et al. 2015; Smith et al. 2016). Although it is a double challenge, understanding how differences in network structure before and after the invasion impact our ability to manage them is a first step towards an informed recovery.

A control theoretical approach not only might provide insight to conservation but also for ecological science: by explicitly taking into account the extent to which changes in the abbundances of one species may ripple trough the community, applying control theory to ecological networks can provide an indication of which species are important from a dynamic perspective, and therefore crucial when attempting to alter (or maintain) the ecosystem state. Nevertheless, although it has been prevoiously used to highlight the disproportionate influence that humans have on marine food-webs (Isbell and Loreau 2013), control theory has has rarely been aplied in an ecological context. reason might be that the control of complex networks is still a young field and the tools necessary to account for variation on the strength of interspecific effects, which are characteristic of ecological networks, are not there.

Here, we expand previous theory of the control of complex systems and use a set of ten paired invaded and uninvaded plant-pollinator communities to investigate the link between network structure and our ability to manage them. We focus on biotic invasions because they can produce tractable changes in the structure of ecological networks. These changes can be particularly pronounced in mutualistic networks of 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, Eskildsen, and Venkatasamy 2002; Aizen, Morales, and Morales 2008; Bartomeus, Vilà, and Santan 2008; Vilà et al. 2009; Traveset et al. 2013). In addition plant-pollinator networks provide an ideal framework to answer these questions. On one hand, community networks that quantify relative levels of interaction are readily available. On the other, the bipartite nature of pollination networks makes it is possible to simplify assumptions of how these interactions translate into interspecific effects. Specifically we ask two key questions framed in the context of a plant invasion. First, we quantify the manaceability of pollination communities. 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.
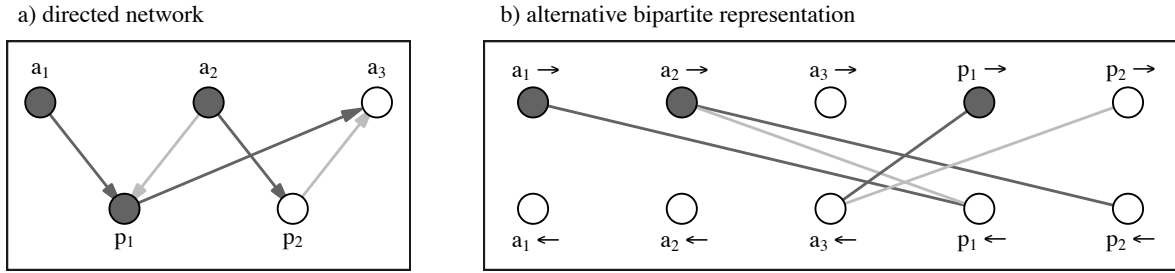
Figure 1: Finding a maximum matching in a complex network. a) We start with a directed network in which the direction of the link represent the direction of control. This is, a link from a_1 to p_1 indicates that the state of p_1 (density/abundances in an ecological context) are influenced by the state of a_1. b) To facilitate the computation of the maximum matching, we can use an alternative representation of the directed network in which each node in (a) is represented by two nodes that indicate their outgoing and incoming links. In both (a) and (b) we show one of the possible maximum matchings of a network (dark grey links) that defines a set of matched (p_1, p_2, and a_3), unmatched (a_1 and a_2) and superior nodes (a_1, a_2, and p_1; dark grey circles). The minimum number of species neccessary to control this network equates to the number of unmatched nodes $n_d = 2$, which gives a manageability of $m = 0.8$.

Theory of community manageability

Maximum matching

The number of nodes necessary to fully control a complex network can be calculated by counting the number of unmatched nodes in the network's maximum matching (Liu, Slotine, and Barabási 2011). In a directed network, a given matching is a subset of links in which no two links share a common starting node or a common ending node; a node is then matched if it is the ending node of one of the links in the matching and unmatched otherwise(Figure 1a). A given matching is then maximum if both *(i)* the number of matched links—known as matching size—is maximal and *(ii)* the sum of the weights of the matched links—known as matching weight—is the largest possible among all possible matchings of that size (West 2001). To find the maximum matching, we it is useful to adopt an alternative bipartite representation of the network in which the two levels indicate the outgoing and incoming links to each node (Figure 1b). Finding a matching in this alternative representation is equivalent to finding a set of links such that each node on the top level is matched to at most one node on the bottom level, and vice versa (West 2001; Csardi and Nepusz 2006).

Given a maximum matching, the link to network controllability has an intuitive basis. In control theory, a network is fully controlable when each node has a "superior", that is, an input that drives its dynamics. Consequently, each matched nodes can be controled by the node pointing to it. Unmatched nodes, on the other hand, have no superior in the network and must be directly controlled by external inputs (Liu, Slotine, and Barabási 2011). In an ecological context, this is what we refer to as management interventions. Building on this, systems that require a large number of external inputs are more difficult or costly to control. Therefore, the manageability *m* of a community can be approximated by the proportion of species on which we would need to apply management interventions in order to gain full control of the abundances of *all*

species in the ecological community

$$m = 1 - \frac{n_d}{s},$$

where m ranges between zero and one, n_d is the number of species needed to gain full control and s is the total number of species in the community.

Relative importance

The manageability of a community m provides an indication of the magnitude of n_d but not the identity of the species that compose this set. This is rather important since maximum matchings are often not unique in for a given network and different sets of species of size n_d could potentially be used to control the network (Liu, Slotine, and Barabási 2011). Species vary in terms of the frequency with which they are classified as superior nodes (Figure 1), and this frequency provides an indication of their relative importance in driving the state of the community. Ecologically, these distinctions are crucial because resources are limited and therefore ecological inteventions should be focused on species that might provide the largest impact. As superior nodes Figure 1 drive the dynamics of other species and are therefore important for the controlability of the network because they either require external input or because the are part of the chain that transmit the external imputs to other species, we therefore call *driver species* those that are identified as being a superior node in all possible matchings, and hence those most likely to have a disproportionate effect on the abundances of other species in their community.

As previously described, a maximum matching in a weighted network is one whose links have the largest possible total weight among all possible matchings. One way to calculate the species importance, and identify the driver species, would be to consider only maximum matchings. However empirical intraction strengths are to some extent stochastic and depend on proximate factors such as sampling method and intensity (Rezende et al. 2007). This means that in weighted networks there is a number of matchings that have maximal size, but are not maximum matchings because their total weight is not maximal. We therefore relaxed the matching weight requirement and computed all possible matchings in the network that have the same maximal size while allowing for some tolerance regarding the weight. To compute all the matchings with maximal size, we first generated the network's line graph—another representation in which nodes are the links of the original network and links represent common ending points (West 2001). We then calculated the complement of the line graph: a graph in which nodes are connected if and only if they are not connected in the line graph. All possible matchings of maximal size can be found by enumerating all cliques (subgraphs in which every node is linked to every other) of maximum size, which equates to $1 - n_d$m in this complement graph (Csardi and Nepusz 2006; Gutin 2013).

Methods

In the last section, we outlined the theoretical and computational underpinings of our approach. Now we illustrate its empirical application using ten pairs of plant-pollinator communities for which we explored their manageability and the relative importance of their constituent species. The networks were constructed from previously published visitation data collected from pollination communities in Bristol, UK (Lopezaraiza-Mikel et al. 2007) and in Cap de Creus National Park, Spain (Bartomeus, Vilà, and Santamaría 2008). Notably, each network pair was composed of a community invaded by a plant and a community "free" of the invasive species (Table S1). In the four British uninvaded communities, the non-invaded plots were obtained by experimentally removing all the flowers of the invasive species *Impatients grandulifera*. In contrast, the Spanish uninvaded communities were obtained from plots that had not yet been colonised by either of the invasive species *Carpobrotus affine acinaciformis* or *Opuntia stricta*. The structure of these networks was determined using visitation frequency which has been shown to be an appropriate surrogate for interspecific effects in pollination networks (Vázquez, Morris, and Jordano 2005; Bascompte, Jordano, and Olesen 2006). To examine whether this decision would influence our results, we also evaluated the effect of using pollinator efficiency or importance as alternative measures of species interactions in a different dataset (Ne'Eman et al. 2010; Ballantyne, Baldock, and Willmer 2015), and we found quantitatively results for all of these options (see Supplementary Information).

Weighting & directing links

Recall that the aforementioned maximum matching algorithm 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 in consistent with the dynamics of the comunity. In some ecological networks, establishing a directionality is relatively straightforward, for example when links represent biomass transfer or energy flow. 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 (Bascompte, Jordano, and Olesen 2006). The dependency 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 dependency of pollinator j on plant i, d_{ji}, is the ratio of the visits by pollinator j to plant i and all visits of pollinator j. As the dependencies are bidirectional, adopting this assumption generates a weighted bipartite network in which interacting pairs are connected by two directed links (Figure 2b).

Mutual dependencies have been shown to be highly assymetric in natural communities (Bascompte, Jordano, and Olesen 2006); in other words, if a plant species is largely dependent on a pollinator species,
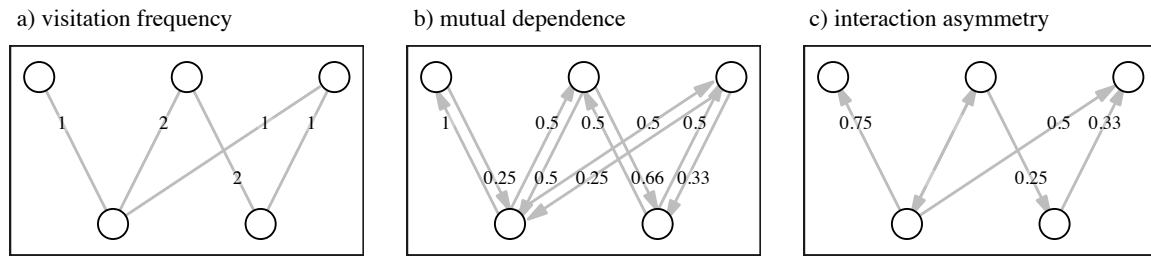
Figure 2: Different ways to depict quantitative mutualistic networks. a) Pollination networks are usually described by the number of visits between each plant and animal species. b) Given visitation data the mutual dependencies between interacting species depend directly on the relative visitation frequency. c) The relative differences of dependencies—the interaction asymmetry—then provides a mean to simplify the interspecific effects.

then that pollinator tends to depend rather weakly on the plant. This suggests that it may be possible to relax the assumption of bidirectional dependences and simplify the network further such that interacting species are only connected by one directed link when mutual dependencies are assymetric (Figure 2c). The extent to which a species i affects species j relative to the extent to which species j affects species i can be summarised by the interaction asymmetry given by

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

Employing an unidrectional interaction asymmetry, as a surrogate of bidirectional mutual dependences, dramatically reduces the number of links in the network, which provides substantial reduction of the time and memory required for the computation of of all posible maximum matchings in a network, particularly for large networks (see "relative importance of species" subsection below).

Community manageability

Given the different networks, we started by quantifying their manageability. To do so, we calculated the maximum matching of the corresponding pollination network, and estimated the minimum number of species that need directed intervecntions to fully control the species abbundances in the community. If a network had more than one component (two species are in different components if there exists no path between them), we only analysed the largest one. Although understanding the variability of manageability across ecological networks is an useful result itself, we also wanted to test whether network attributes, like invasion status, have an impact on the observed manageability values. We therefore used a set of generalised linear models (with binomial error structure) to investigate the effect of invasion status while controlling for factors related to species richness, since one might naively expect to see a negative relationship between diversity and manageability (Menge 1995). These covariates inlcuded the total number of species, plant richness, polinators richness, the ratio of plants to pollinators richness, and the study site. We assessed competing models by comparing the Akaike Information Criterion corrected for small sample sizes (AICc), and report

148 results for the most parsimonious one.

149 We next explored the extent to which structural properties of the empirical networks influence their
150 manageability. Previous research indicates a direct link between a network's degree distribution and the
151 number of nodes necessary to fully control it (Liu, Slotine, and Barabási 2011), but the strength and
152 applicability of this relationship has not been tested for in weighted ecological networks. We therefore
153 compared the manageability of the empirical networks to networks generated by three null models which
154 varied in terms of the constraints they impose. The first set of random visitation networks maintain the
155 connectivity of the empirical network, but both degree (its number of interactions) and strength (its total sum
156 of visits) were allowed to vary. A second set set was generated by maintaining each species' degree while
157 varying the number of visits per species. Finally a third set of random networks mantained the species'
158 strength while varying their degrees. Randomisations were generated using vegan 2.3-3 (Oksansen et al.
159 2016). After generating the randomized networks under these three schemes, we then calculated the mutual
160 dependences and interaction asymmetries of each and determined their manageability using the maximum
161 matching algorithm. Finally we calculated the average rank (akin to a p-value) of the manageability of each
162 empirical network compared to the corresponding manageabilites of each set of 999 randomisations.

163 The dependency asymmetry plays a fundamental role in determining the direction of control in each two-
164 species interaction and therefore has the potential to influence the network manageability results above. We
165 therefore performed an additional randomisation in which we kept the structure of network consistent but
166 randomised the direction of the interaction asymmetries. That is, we first calculated the assymetries for each
167 community and then shuffled the direction of the link between species. Similar as in previous null models,
168 we calculated the average rank of the empirical manageability as compared to those of the randomisations.

Relative importance of species

170 Our second key question is related to how different species differ in their importance for the population
171 dynamics of the community. To quantify this importance in each network, we computed all possible match-
172 ings that have the same size as the networks' maximum matching. We then calculated the frequency with
173 which each species is deemed to be a superior node in the set of matchings that had a total weight greater
174 or equal to 0.5 times the weight of the maximum matching. We selected this threshold as it provided a
175 high agreement between networks quantified by visitation and pollination efficiency as well as between our
176 weighting/directionality assumptions (mutual dependences and inetraction asymmetries); however the choice
177 of this threshold had a negligible impact on the results (Supplementary Information).

178 Even in sparse networks, like these studied here, the number of maximal matchings increases exponen-
179 tially with the number of links and nodes in a network. Unfortunately, this means that the large number
180 of links in the most diverse communities rendered the computation unfeasible when we used mutual depen-

decies. Taking this limitation into account, we compared the relative network manageability obtained when using asymmetries to those found when using mutual dependencies for eleven of the twenty networks (those for which the number of matchings was smaller than 4×10^{10}). The comparison was performed using a paired Spearman correlation test, a weighted correlation coefficient r_{w2} (which gives more weight to higer ranks; Pinto Da Costa, Roque, and Soares 2015), and a Jaccard similarity of the driver species in both approaches. All three approaches identified a high similarity in relative ranks. Therefore, we used the results from the asymetries, rather than mutual dependences, to further investigate the factors that determine species' relative importance since this also allows us to obtain results for all networks.

Given the species importance obtained using the interaction asymmetries, we then asked the question of whether some species-level structural properties can predict the relative importance of species. To do so, we used a generalised linear mixed-effects model (GLMM) with a logistic link function to evaluate the relationship between the species' relative importance and a suite of structural measures. As predictors in this model, we specifically included measures of centrality (degree and eigen-centrality), which have been found to be strong predictors of importance in a coextintion context (Memmott, Waser, and 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); and measures of strength of association and dependence (visitation and dependency strength), as their distribution determine the extent of interspecific effects; and whether the species was invasive or not. In addition we also included guild and invasive status as fixed effects; although the importance of plants and pollinators or invasive and non-invasive species could respond differently to our structural metrics, our dataset did not contain enough variation to include the corresponding interactions terms. All metrics were calculated using the R package bipartite 2.06 (Dormann, Gruber, and Fründ 2008). We allowed for variation between different communities by including the network identity as a random effect (Bates et al. 2015). 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 and Anderson 2003; Bates et al. 2014; Barto 2016).

Results

Community manageability

The studyed networks had levels of manageability between 0.12 and 0.58 (mean 0.37) when we considered bidirectional links weighted by the mutual dependences. This was in strong agreement to the results obtained using the dependence asymmetry in which manageability ranged between 0.08 and 0.45 (Spearman rank correlation 0.93, $p = 1.7 \times 10^{-9}$). In addition we found that even when controling for diversity, invaded
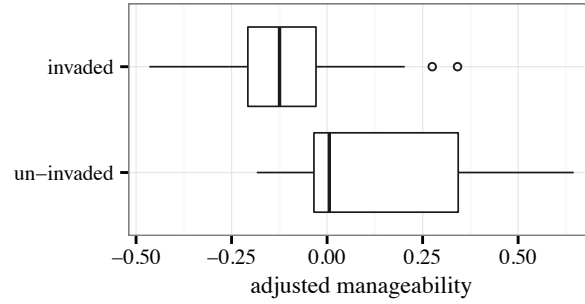
<div align="center">8</div>

Figure 3: Invaded communities have lower levels of manageability than uninvaded communities even when controling for the ratio of plant to pollinator richness. Adjusted manageability corrsponds to the partial working residuals of the invasion status. The box covers the 25th75th percentiles, the middle line marks the median, and the maximum length of the whiskers is 1.5 times the interquartile range. Points outside this range show up as outliers.
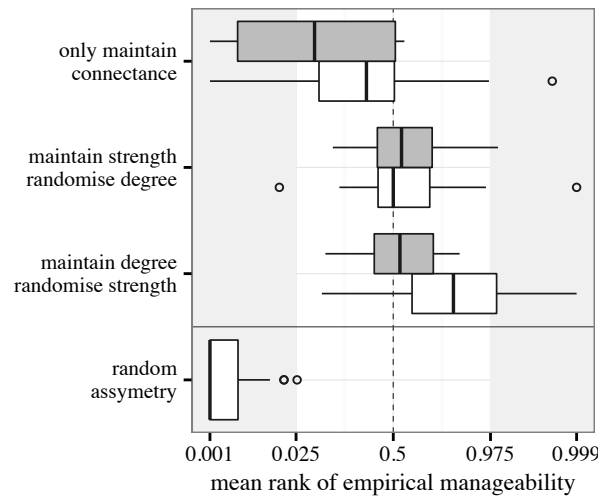

Figure 4: The manageability of empirical networks was compared to network randomisations using a normalised rank. The shaded areas in light grey (< 0.025 and > 0.975) suggest a significant difference between the empirical network and its randomisations. The empirical manageability is much smaller than those of randomisations in which the direction of assymmetries has been randomised. In contrast the manageability of network in which the visitation strength or degree was mantained was not different to the manageability of the empirical networks. Dark grey and white boxplots represent manageabilities obtained using mutual dependencies and asymmetries respectively. All boxes are as in Figure 3.

213 communities ~~had~~ were more difficult to manage than uninvaded ones. Out of the explored factors—total

214 number of species, plant richness, pollinator richness and the ratio of plant to pollinator richness—only the

215 ratio of plants to pollinator was retained in the final model (as determined by the AICc; Figure 3, Table S3).

216   The manageability of empirical networks was, in general, not significantly different to the manageability of

217 network randomisations that maintain the degree or the strength of individual species (Figure 4). However

218 when comparing the empirical network to less constrained randomisations that maintained the original

219 connectance but in which species had different degrees and strengths, we found that empirical networks tend

220 to have smaller values of manageability. This pattern is even more marked when we maintained the network

221 structure but randomised only the direction of the asymmetries (Figure 4).

factor	est.	No. mod.	imp.	C.I.
(Intercept)	3.07	15	1.00	2.01
dependency strength	36.29	15	1.00	14.16
visitation strength	1.41	15	1.00	1.10
contribution to nestedness	1.29	15	1.00	1.11
degree	0.73	7	0.40	3.09
eigen-centrality	-0.08	7	0.35	0.41
guild (pollinator)	0.20	7	0.30	1.23
invasive sp.	-9.01	7	0.26	27959.48

Table 1: The strength of dependency, contribution to nestedness and visitation strength had a significative effect on all the models that accounted for 95% of the evidence based on AICc. Coeficient estimates were avaraged following Buckland, Burnham, and Augustin (1997); confidence intervals were calculated following Lukacs, Burnham, and Anderson (2010).

Relative importance of species

We found a strong agreement between relative species' importance in the 11 networks for which we were able to calulate it using both mutual dependencies and asymmetries (Spearman's rank correlation ranged between $\rho = [0.6, 0.78]$, median $\tilde{\rho} = 0.69$). Indeed, when using the weighted rank correlation coefficient r_{w2}, we found that the agreement was stronger for highly ranked species than for lowly ranked species ($\tilde{r_{w2}} = 0.72$ versus $\tilde{r_{w2}} = 0.59$). Moreover both approaches identified a highly similar set of driver species (Jaccard similarity $J = [0.5, 1]$, $\tilde{J} = 0.67$). Therefore we employed the relative rankings obtained using asymmetries in the following analyses.

Although plants showed significantly higher levels of importance than pollinators (Mann-Withney-Wilcoxon test, $p0$), this difference can be largely explained by the strength of dependency of the species (the sum of the dependencies for a given species). Indeed, when averaging over the set of GLMMs that accounted at least 95% of the evidencee based on AICc, we found that the strength of dependency is the single most important factor determining the relative importance of species for network control (Table 1, Figure 5). In contrast, the number of visits a species makes (or receives) and its contribution to nestedness have only a marginal effect on its relative importance.

Discussion

Our results reveal that invasive mutualists are driver species in the communities they invade. As driver species, they occupy a dominant role in which changes on their abbundance have the potential to cascade trough the community and in turn affect the abbundances of several other species in the community. They achieve that by altering the distribution of the strength of mutual dependencies and the interaction asymmetries—which constitute the foundations of the structure of mutualistic networks (Vázquez and Aizen 2004; Bascompte, Jordano, and Olesen 2006). Furthermore, these structural differences caused by invasive species at a community level are reflected in a potential decrease in our ability to alter the state of the
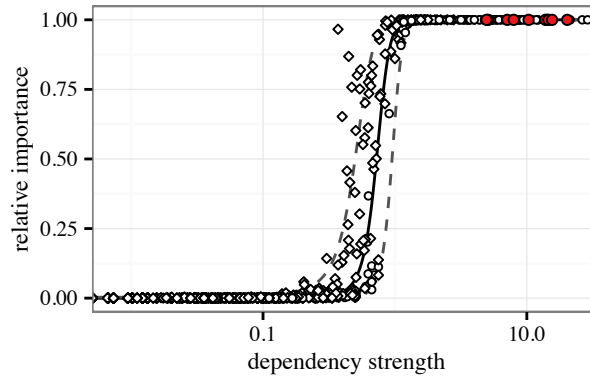
Figure 5: Dependency strength is the single most important factor explaining the importance of species for network control. Visitation levels and contribution to nestedness had a significant albeit small effect on the importance (dashed lines correspond to ±one standard deviation on these factors). Invasive species (red) were invariably classified as driver species (those having the maximum importance for network control.

community.

We confirm previous studies that suggested that in contrast with other kind of complex networks, the structure of ecological networks renders them remarkably difficult to control (Liu, Slotine, and Barabási 2011; Ruths and Ruths 2014). In a hypothetical situation in which the goal were to regulate the abbundances of all species in a pollination community, our results suggest that we would need to directly intervene the abbundances of at least 40-90% of those species. Fully controling an ecological community is out of the question, as designing and implementating the management interventions needed is currently impractical. Nevertheless, the "manageability" of an ecological community, which is related to the number of species that would require a directed intervention, can 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.

Asymmertic depedences have previously found to be related to the stability and persistence of pollination networks (Memmott, Waser, and Price 2004; Vázquez and Aizen 2004; Lever et al. 2014; Astegiano et al. 2015). Here, we demonstrate that the manageability of mutualistic networks is also governed by the asymetric nature of mutual dependeces. Indeed, our empirical networks have markedly lower levels of manageability compared to randomisations in which the visitation network was unchanged, but the patterns of dependence were broken by randomising the direction of the asymmetries. However, consistent with previous results (Liu, Slotine, and Barabási 2011), we show that the manageability of empirical networks was indistinguishable from that of networks with a random structure (in terms of modularity and nestedness for example) but that maintained the degree or strength of each species in the community. This suggest that the asymmetries at the species (specialization-generalization asymmetries) and the link level (interaction's dependence asymmetries) appear to be sufficiently defined by the distribution of species degree and strength (Melián and Bascompte 2002). Furthermore, we found that invasive species, by altering the patterns of assymetry, reduce the manageability of their communities (Henriksson et al. 2016). This result is in agreement with previous

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studies that suggest that invasors erode native pollination webs by ursurpating interactions and exarcerbate the asymmerties in the network, which in turn might increasse the stability of the community (Aizen, Morales, and Morales 2008; Bartomeus, Vilà, and Santamaría 2008).

The changes on the asymmetries found in the invaded networks are not only reflected in the manageability at a community level: invaders were found to be driver species in every single community which they were present. Invasive plants have usually been found to be super-generalists thus playing a central role in their networks (Vilà et al. 2009; Palacio, Valderrama-Ardila, and Kattan 2016). Nevertheless, we found that dependence strength, rather than generalism or other metrics of centrality, explains best the importance of species for the community dynamics. Specifically, driver species tend to be those whose interaction partners are collectively more dependent on them than the other way arround. However, the influence of dependence strength was held regardless of wheter the species was invasive or not, which corroborates previous observations that suggest that exotic species, although having different traits, are not inherently different to their native counterparts, but are rather governed by the same rules of niche and competition that determine species coexistence (Stouffer, Cirtwill, and Bascompte 2014). Invasive species have been shown to have the ability to transform the structure of ecological communities (Aizen, Morales, and Morales 2008; Albrecht et al. 2014), our results suggest that they also may have the ability to heavily influence the abbundances of other species in the ecosystem.

Because of their effects on other species in the community, driver species might be natural candidates for management interventions. For instance, despite inconsistent outcomes, 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 executed with caution as invaded commmunities tend to be dependent on them and therefore vulnerable to their erradication (Traveset et al. 2013; Albrecht et al. 2014). Although useful for identifying conservation priorities, our approach is different to previous attempts to quantify species importance that concentrate on measures of centrality, position, coextintion or uniqueness (Jordán, Liu, and Davis 2006; Jordán 2009; Lai, Liu, and Jordan 2012; McDonald-Madden et al. 2016). Instead the concept of driver species is more akin to the original concept of keystone species, which illustrated how changes on the abbundance of a key species in turn affect the abbundances of other members of the community (Paine 1969; Paine 1995). However, while the keystone species were traditionally identified by infering the effects of a perturbation on a community's population dynamics (Mills and Doak 1993), the driver species concept operates the other way round, and uses the communuty dynamics, underpinned by the interspecific effects, to infer the effects of a perturbation. While it is challenging to quantify the dependence of species in an ecological community, an experimental approach to identofy dynamically important species might be even more difficult.

Here we ilustrate how a control theoretic approach can be used to study the effect on mutualistic communities of a major driver of global change, however it can be easily extended to understand the structural

effects of other kind of preturbations and species interactions. Moreover, we see great potential by explicitly integrating control theory with dynamics models of species densities (Cornelius, Kath, and Motter 2013; Gibson et al. 2016). From an ecological perspective, it can provide key insight on determining the relationship between controlability and species coexistence, as well as determining the trade-offs between persistence at the species and the community level. From a conservation perspective, a combined approach can be useful, not only to idetify ideal targets for management interventions, but also to design informed, rather than hopeful, interventions that achieve restoration goals.

Acknoledgements

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