

STRUCTURAL CONTROLABILITY OF POLLINATION NETWORKS

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Alternative titles:

STRUCTURAL CONTROLABILITY OF ECOLOGICAL NETWORKS

NETWORK MANAGEABILITY IN THE CONTEXT OF SPECIES INVASION

BIOTIC INVASIONS REDUCE MANAGEABILITY OF ECOLOGICAL NETWORKS

IDENTIFYING THE “DRIVER SPECIES” OF AN ECOSYSTEM

Introduction

Tentative spiel for the first paragraph: We need to manage ecological communities because of ecosystem services and biodiversity maintenance. We would like to control communities in the sense of conserving and restoring them. However to control them (in that sense) we need to understand how species affect each other and potentially the whole system when they are faced by perturbations or management interventions. But we cannot do that yet because we lack a theoretical framework that link the dynamics of the community to management. Control theory might provide this link.

Seminal work on control theory has established a strong link between the structure of complex networks and its controlability and that in principle it is possible to alter any ecological community’s composition, by modifying the abundances of just some key species (Liu, Slotine, and Barabási 2011; Cornelius, Kath, and Motter 2013). Based on this work and using a small number of binary food-webs (only presence or absence of interactions), 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 2014). This theoretical result is in agreement with many cases in which the management of ecological communities is more challenging than anticipated. In contrast with other types of complex systems like neural, intra-organizational, or trust networks, 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. Although

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these conceptual advances on control theory have provided an initial link between the structure of ecological communities and our ability to manage them, this relationship is still ambiguous. Ultimately, the challenge of ecological networks is represented by the variability of their structure and interaction strengths—which can vary by several orders of magnitude.

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For instance, biotic invasions, as other 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). 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, Eklundsen, and Venkatasamy 2002; Aizen, Morales, and Morales 2008; Bartomeus, Vilà, and Santamaría 2008; Vilà et al. 2009; Traveset et al. 2013). Moreover, as evidenced by the limited amount of success of restoration projects (Smith et al. 2016), returning invaded communities to a predisturbance state is quite a difficult endeavour (Suding, Gross, and Houseman 2004; Rodewald et al. 2015). Understanding how invasion-induced differences in network structure impact our ability to manage them, can provide useful lessons to conservation science. What is more, there are also ecological insights to be had: by explicitly taking into account the extent to which changes in the abundances of one species may ripple through 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.

Isbell and Loreau (2013) used a control theoretic approach to find the minimum subset of species necessary to maintain network structure in six marine food webs. They found that humans affect a larger proportion of this subset of species than, for instance, apex predators. They argue that this disproportionate influence could translate into unintentional restructuring of food webs. Although insightful, the scope and applicability of Isbell and Loreau (2013) can be extended in numerous ways. First, although they find the size of this minimum set, they disregard the fact that the set species composition is not unique and thus not all species that might be included are equally important for the community population dynamics. Second, their methods were naive to differences on the strength of interspecific effects. And third, their approach was conceptually limited to trophic interactions.

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Here, we expand previous theory of the control of complex systems and use a set of paired invaded and uninvaded plant-pollinator communities to investigate the link between network structure and our ability to manage them. 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. Our theoretical extension of network control, allow us to ask the question of whether biotic invasions as drivers of change in network structure increases or decreases the manageability of communities as well as the relative importance of species at driving the population

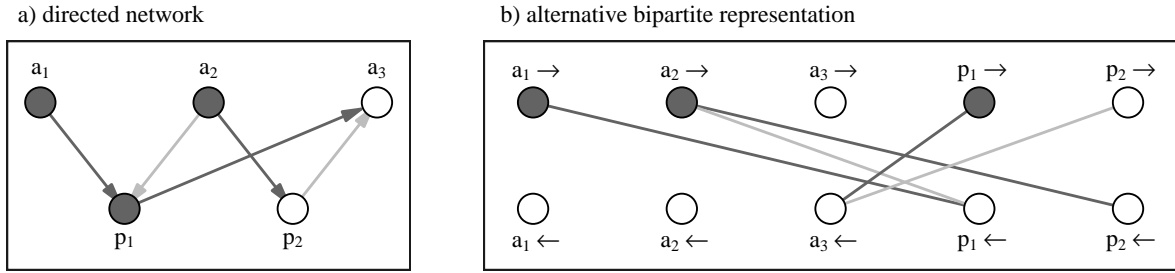


Figure 1: Finding a maximum matching in a complex network. a) We start with a directed network in which the direction of the link represent the direction of control. This is, a link from a_1 to p_1 indicates that the state of p_1 (density/abundances in an ecological context) are influenced by the state of a_1 . b) To facilitate the computation of the maximum matching, we used an alternative undirected bipartite representation of the directed network in which each node in (a) is represented by two nodes that indicate the outgoing and incoming links. One of the possible maximum matchings of a network (dark grey links) defines a set matched (p_1 , p_2 , and a_3) and unmatched nodes (a_1 and a_2). The minimum number of species necessary to control this network equates to the number of unmatched nodes $n_d = 2$. Superior nodes (dark grey circles) drive the dynamics of other species and are therefore important for the controllability of the network because they either require external input or because they are part of the chain that transmit the external inputs to other species.

dynamics of other species in the community. .

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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 matched if it is the ending node of one of the links in the matching (Figure 1a). A 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 used 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 a relatively straightforward and intuitive basis. In control theory, a network is fully controllable when each node has a “superior”, that is, an input that drives its dynamics. Matched nodes can thus be controlled 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.

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 n_d is the proportion of species needed to gain full control and s is the total number of species in the community.

Weighting & directing links

Recall that our 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 establish a directionality for the links between species that is consistent with the dynamics of the community. In some ecological networks, establishing a directionality is relatively straightforward when they represent resources or energy flow. Interspecific effects in pollination networks, however, are not strictly directed. Nevertheless, the extent to which a pair of interacting species affect each other can be quantified by the magnitude of the mutual dependence (Bascompte, Jordano, and Oelsen 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 asymmetric in natural communities (Bascompte, Jordano, and Oelsen 2006). In other words, if a plant species is largely dependent on a pollinator species, then the pollinator tends to depend only very weakly on the plant. This suggests that it may be possible to relax this initial assumption and simplify the network further such that interacting species are only connected by one directed link when mutual dependencies are asymmetric (Figure 2c). The extent to which a species i affects species j relative to the extent to which species j affects species i can then be summarised by the interaction asymmetry

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

Employing an unidirectional interaction asymmetry, as a surrogate of bidirectional mutual dependences, dramatically reduces the number of links in the network. Which dramatically simplifies the computation of all possible maximum matchings in a network.

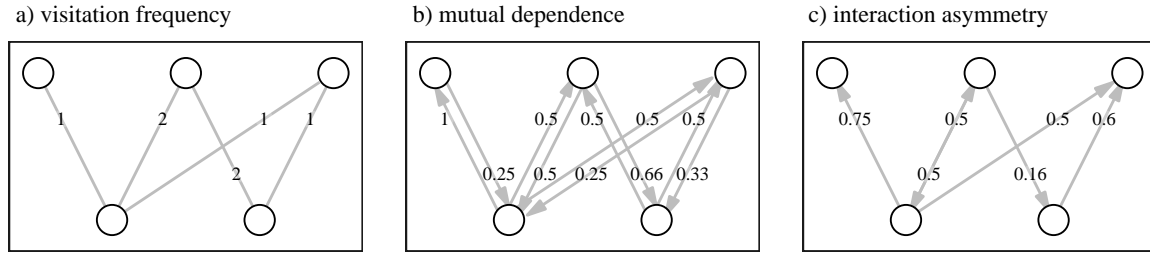


Figure 2: Different ways to depict quantitative mutualistic networks. a) Pollination networks are usually described by the number of visits between each plant and animal species. b) Given visitation data the mutual dependencies between interacting species depend directly on the relative visitation frequency. c) The relative differences of dependencies—the interaction asymmetry—then provides a mean to simplify the interspecific effects.

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. Moreover, maximum matchings are often not unique in for a given network and different sets of species of size n_d could 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 interventions should be focused on species that might provide the largest impact. We therefore call *driver species* those that are identified as being a superior node in all possible matchings, and consequently likely to have the most disproportionate effect on the abundances of other species in their community.

As previously described, unlike unweighted networks, where a maximum matching is defined solely by its matching size, a maximum matching in a weighted network is one whose links have the largest possible total weight among all possible matchings. This means that in weighted networks there is a number of matchings that have maximal size, but are not maximum matchings because their total weight is not maximal. One alternative to calculate the species importance, and identify the driver species, would be to consider only maximum matchings. However empirical intreaction strengths, from which we calculate dependencies, are to some extent stochastic and depend on the sampling method and intensity. We therefore relaxed the matching weight requirement 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—an alternative representation in which nodes are the links of the original network and links represent common ending points. We then calculated the complement of the line graph: a graph in which nodes are 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 of size $1 - n_d$ in this complement graph (West 2001; Csardi and Nepusz 2006).

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 *Impatiens 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 Oelsen 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 (Ne’Eman et al. 2010; Ballantyne, Baldock, and Willmer 2015), and we found quantitatively results for all of these options (see Supplementary Information).

All analysis were performed in R 3.2.2 (R Core Team 2015).

Community manageability

Given the different networks, we started by quantifying their manageability. To do that, 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 abundances 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 perturbations, like invasion status, have an impact on 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—as naively one might expect to see a negative relationship between diversity and manageability (Menge 1995). Coovariates 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).

We next explored the extent to which structural properties of the empirical networks influence their

manageability. Previous research indicates a direct link between a network’s degree distribution and the number of nodes necessary to fully control it (Liu, Slotine, and Barabási 2011), but the strength and applicability of this relationship has not been tested for in weighted ecological networks. We therefore compared the manageability of the empirical networks to networks generated by three null models which varied in terms of the constraints they impose. The first set of random visitation networks maintain the connectivity of the empirical network, but both degree and weight were allowed to vary. A second set was generated by maintaining each species’ degree (its number of interactions) while varying the number of visits per species. Finally a third set of random networks maintained the species’ strength (its total sum of visits) while varying their degrees. Randomisations were generated using *vegan* 2.3-3 (Oksanen et al. 2016). After generating the randomized networks under these three schemes, we then calculated the mutual dependences and interaction asymmetries and determined their manageability using the maximum matching algorithm. Finally we calculated the p-value of the manageability of each empirical network and the corresponding manageability of 999 randomisations.

The dependency asymmetry plays a fundamental role in determining the direction of control in a two species interaction and therefore has the potential to structure the network matching. We therefore performed an additional randomisation in which we maintained the structure of network but randomised the direction of the interaction asymmetries. This is, we first calculated the asymmetries for each community and then shuffled the direction of the link between species. Similar as in previous null models, we calculated the p-value of the empirical manageability compared to that of the randomisations.

Relative importance of species

Our second key question is related to how different species differ in their importance for the population dynamics of the community. To quantify this importance in each network, we computed all possible matchings that have the same size as the networks’ maximum matching. We then calculated the frequency to which each species is deemed to be a superior node in matchings with a weight greater or equal to 0.5 times the weight of the maximum matching. We choosed this threshold as it provided a high agreement between networks quantified by visitation and pollination efficiency as well as between our weighting/directionality assumptions (mutual dependences and interaction asymmetries). Note that the choice of this threshold had a negligible impact on the results (Supplementary information).

We observed that the number of maximal matchings increases exponentially with the number of links and nodes in a network. Unfortunately, this implies that the large number of links in the most diverse communities renders the computation unfeasible when we use mutual dependencies. Taking this limitation into account, we compared the relative network manageability obtained when using asymmetries or when using mutual dependencies for eleven of the twenty networks—for which the number of matchings was smaller than 4×10^{10} . The comparison was performed using paired Spearman correlation test, a weighted

correlation coefficient r_{w2} —which gives more weight to higher ranks (Pinto Da Costa, Roque, and Soares 2015), and a Jaccard similarity of the driver species in both approaches. All three approaches suggested high similarity in relative ranks. Therefore, we used the results from the asymmetries, rather than mutual dependences, to further investigate the factors that determine species' relative importance.

Given the species frequency 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) to evaluate the relationship between the species' relative importance and a suite of structural measures. We specifically included measures of centrality (degree and eigen-centrality) which have been found to be strong predictors of importance in a coextinction context; measures 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 skewed distribution is characteristic of plant-pollinator networks and determine the extent of interspecific effects. All metrics were calculated using the R package bipartite 2.06 (Dormann, Gruber, and Fründ 2008). We allowed for variation among different communities by including the network identity as a random effect (Bates2015a). 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).

Invasive species have been shown to have disproportionate effects on the communities they invade. So we lastly examined the extent to which invasive species tend to be driver species—species with the maximum importance—and to which extent their importance could be explained by the factors previously described. To do so, as our invasive species were plants, we first used a Mann-Whitney U test to compare the relative importance of invasive species to those of other plants in the community. We then examined the residuals of the GLMM to investigate if invasive species' importance is larger or smaller than expected given their network structural properties.

Results

Community manageability

The studied 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 controlling for diversity, invaded communities had were more difficult to manage than uninvaded ones. Out of the explored factors—total

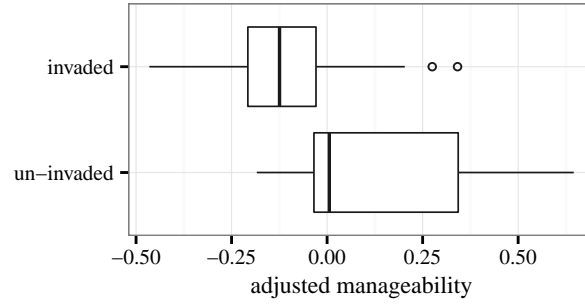


Figure 3: Invaded communities have lower levels of manageability than uninvaded communities even when controlling for the ratio of plant to pollinator richness. Adjusted manageability corresponds to the partial working residuals of the invasion status.

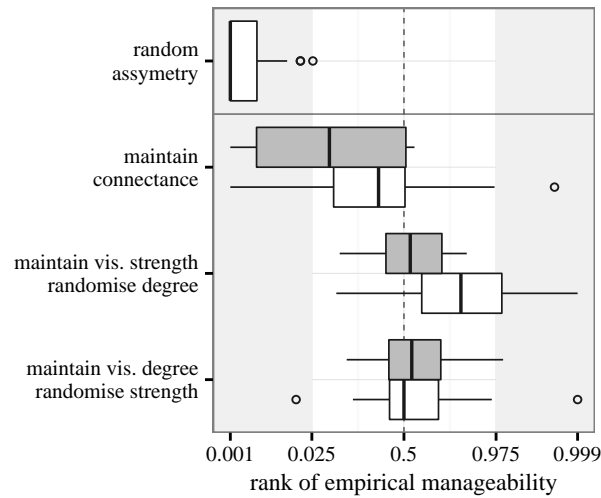


Figure 4: The manageability of empirical networks was compared to network randomisations using a normalised rank. The shaded areas in light grey (< 0.025 and > 0.975) suggest a significant difference between the empirical network and its randomisations. The empirical manageability is much smaller than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

number of species, plant richness, pollinator richness and the ratio of plant to pollinator richness—only the ratio of plants to pollinator was retained in the final model (as determined by the AICc; Figure 3, Table S3).

The manageability of empirical networks was, in general, not significantly different to the manageability of network randomisations that maintain the degree or the strength of individual species (Figure 4). However when comparing the empirical network to less constrained randomisations that maintained the original connectance but in which species had different degrees and strengths, we found that empirical networks tend to have smaller values of manageability. This pattern is even more marked when we maintained the network structure but randomised only the direction of the asymmetries (Figure 4).

Relative importance of species

We found a strong agreement between relative species' importance in the 11 networks for which we were able to calculate it using both mutual dependencies and asymmetries (Spearman's rank correlation ranged between

factor	est.	No. mod.	imp.	C.I.
(Intercept)	3.20	3	1.00	2.03
dependency strength	37.25	3	1.00	14.82
contribution to nestedness	1.42	3	1.00	1.01
visitation strength	1.38	3	1.00	1.14
eigen-centrality	-0.07	1	0.29	0.39
guild (pollinator)	0.14	1	0.22	0.94

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

$\rho = [0.6, 0.78]$, 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 ($r_{w2} = 0.72$ versus $r_{w2} = 0.59$). 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-Whitney-Wilcoxon test, $p < 0.001$), 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 evidence 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.

In addition, in the ten communities that were invaded, invasive species were invariably classified as a driver species. In general, the relative importance of invasive species was significantly larger than those of the other plants in the studied communities (Mann-Whitney U Test, $p = 0.02$). However this difference can be fully explained by the explanatory variables in our model as all the residuals for the invasive species were virtually zero.

Discussion

We found that

Therefore, full controllability of ecological networks—being able to steer the ecosystem into any desired ecosystem state—would require a This characteristics render ecological networks unlikely to be able to visit every possible system state other closed systems, ecological networks

The controllability of ecological networks is not a concept limited to control theory. Controllability in the ecological context can be seen as a direct measure of the minimum number of species whose abundance would need to be directly regulated to achieve full network control. While we are far away from

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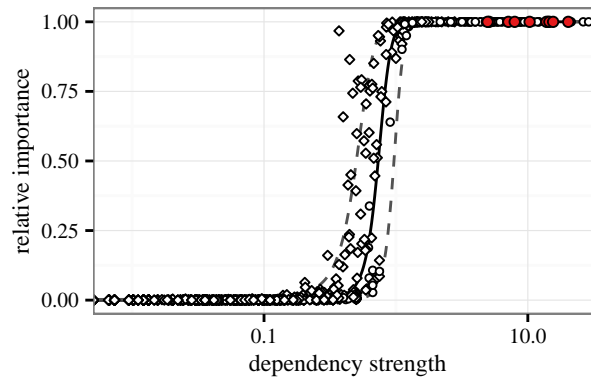


Figure 5: Dependency strength is the single most important factor explaining the importance of species for network control. Visitation levels and contribution to nestedness had a significant albeit small effect on the importance (dashed lines correspond to \pm one standard deviation on these factors). Invasive species (red) were invariably classified as driver species (those having the maximum importance for network control).

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