Biotic invasions reduce the manageability of pollination networks

**E. Fernando Cagua\*, Kate L Wootton§, Daniel B. Stouffer#**

Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8041, New Zealand

\* [efc29@uclive.ac.nz](mailto:efc29@uclive.ac.nz) § [kate.l.wootton@gmail.com](mailto:kate.l.wootton@gmail.com) # [daniel.stouffer@canterbury.ac.nz](mailto:daniel.stouffer@canterbury.ac.nz)

* **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:** ~ 153 abstract; ~ 7490 main text.
* **Number of references:** ~ 61
* **Number of displays:** 5 figures; 1 table.
* **Correspondence to:** Daniel Stouffer ([daniel.stouffer@canterbury.ac.nz](mailto:daniel.stouffer@canterbury.ac.nz)) - +64 3 364 2729 - Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand
* **Authorship:** DBS conceived the idea; EFC, KLW and DBS 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 such as biotic invasions, affect our ability to manage ecological communities. Here, we expand current theory on the controllability of complex systems to quantitatively assess the relative manageability of ten pairs of uninvaded and invaded plant-pollinator communities. Intriguingly, we found that invaded pollination networks might be more resilient than their uninvaded counterparts as they showed substantially lower levels of manageability. We also developed theory to help identify each community's driver species—those most important to manage because of their disproportionate potential to affect the abundances of all other species. Remarkably, invasive plants were found to be driver species in every community in which they were found; their dominant position was generally underpinned by high asymmetry in the dependence of their interaction partners. Our results provide a theoretical explanation for the known challenges associated with the restoration of invaded communities, and also provide insight into the design of informed management interventions.

*Shorter version*: It is generally unknown how the disruptions caused by perturbations like biotic invasions, affect our ability to manage ecological communities. Here, we expand current theory on the controllability of complex systems to assess the theoretical manageability of ten pairs of uninvaded and invaded plant-pollinator communities. We found that invaded pollination networks might be more resilient than their uninvaded counterparts as they showed substantially lower manageability. We also identify each community's driver species—those most important to manage because of their disproportionate potential to affect the abundances of all other species. Remarkably, invasive plants were found to be driver species in every community in which they were found; their dominant position was generally underpinned by high asymmetry in the dependence of their interaction partners. Our results provide a theoretical explanation for the known challenges associated with the restoration of invaded communities, and also provide insight into the design of informed management interventions.

# Introduction

Complex systems are characterised by non-linear relationships in which the whole is 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 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 allow us to explain, predict, and manage ecological communities, particularly when they are faced with perturbations (Solé & Montoya 2001; Green *et al.* 2005). Moreover, such a framework needs to be able to account for their complex structure, and the dynamics that determine the state of each species, and the community as a whole.

Among the various possibilities, control theory appears to be a strong candidate as it is designed to deal with determining and supervising the behavior of general dynamical systems, and is well equipped to deal with the many feedbacks presents in ecological communities (Liu & Barabási 2015). Research in the field has established a strong link between the structure of complex networks and their controllability, while also demonstrating that it is in principle possible to alter a whole ecological community's composition by modifying the abundances of only a few species (Liu *et al.* 2011; Cornelius *et al.* 2013; Ruths & Ruths 2014). 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, they can provide an indication of which species are most relevant from a dynamic perspective, a particularly important feature given that these species should underpin informed attempts to both alter or maintain the ecosystem state.

Despite these advances, the link between the structure of complex networks and our ability to manage and conserve them is still ambiguous (Tylianakis *et al.* 2010). To complicate things further, biotic invasions—a major driver 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). Although understanding how differences in network structure before and after the invasion impact our ability to manage them presents a double challenge, it is a critical first step towards a fully informed recovery. Despite the apparent overlap, a control-theoretic perspective has not been widely adopted in an invasion context. This is perhaps because of a lack of appropriate methodological tools that can account for observed variation on the strength of interspecific effects that are characteristic of ecological networks (Liu *et al.* 2011; Isbell & Loreau 2013).

To bridge this gap, we expand previous theory of the control of complex systems to an ecological context. We then use a set of ten pairs of uninvaded and invaded plant-pollinator communities to investigate the link between invasion, network structure and ecological management. We ask two specific questions framed in the context of a plant invasion. First, 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 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, 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 possible to simplify assumptions of how these interactions translate into interspecific effects.

## Theoretical framework

### Manageability

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 *et al.* 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, it is convenient 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 & Nepusz 2006).

Given a maximum matching, the link to network controllability has a largely intuitive basis. In control theory, a network is fully controllable when each node has a "superior", that is, an input that drives its dynamics. Consequently, each matched nodes can 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 *et al.* 2011). In an ecological context, these external inputs are what could be referred to as management interventions. Building on this analogy, 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. This is given by

where *m* ranges between zero and one, *nd* 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 but not the identity of the species that compose this set. This difference is rather important since maximum matchings are often not unique in a given network and different sets of species of size *nd* could potentially be used to control the network (Liu *et al.* 2011). That is, species vary in terms of the frequency with which they are classified as superior nodes, and this frequency provides an indication of their relative importance in driving the state of the community. Ecologically, these distinctions are relevant because resources are limited and therefore ecological interventions should ideally be focused on species that might provide the largest impact. Superior nodes 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; 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 interaction strengths are to some extent stochastic and depend on proximate factors such as sampling method and intensity (Gibson *et al.* 2011). This implies that there will often be multiple matchings that have maximal size in weighted networks but that are not maximum matchings because their total weight is not maximal. We can accommodate this uncertainty by relaxing the matching weight requirement and computing all possible matchings in the network that have the same maximal size while allowing for some tolerance regarding the weight. One alternative to compute all the matchings with maximal size, is to first generate 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). Then calculate the complement of this line graph, which generates a graph in which nodes are connected if and only if they are not connected in the line graph. Finally, all possible matchings of maximal size can be found by enumerating every clique (subgraphs in which all nodes are fully connected to each other) of maximum size in this complement graph (Csardi & Nepusz 2006; Gutin 2013).

## Methods

In the last section, we outlined the theoretical and computational underpinnings 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 *et al.* 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 all networks was determined using 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 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 data set that lacked invasive species (Ne’Eman *et al.* 2010; Ballantyne *et al.* 2015), and we found quantitatively similar results for all of these options (Supplementary Information S1).

### Community manageability

Given the different networks, we began by quantifying their manageability. To do so, we calculated the maximum matching of the corresponding pollination network, and estimated the minimum proportion of species that need directed interventions to fully control the species abundances in the community. To simplify the analysis, we only considered the largest component in a network if it had more than one (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). 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 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 community. In some ecological networks, establishing the 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 *et al.* 2006). The dependency of plant *i* on pollinator *j*, *dij*, 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*, *dji*, is the ratio of the visits by pollinator *j* to plant *i* and all visits of pollinator *j*. As the dependencies are not symmetric, its use generates a weighted bipartite network in which all interacting pairs are connected by two directed links (Figure 2b).

Given the respective dependences, the extent to which a species affects species *j* relative to the extent to which *j* affects *i* can be summarised by the interaction asymmetry given by

Mutual dependencies have previously been shown to be 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). This suggests that it may be possible to relax the assumption of bidirectional dependences further and simplify the network such that interacting species are connected by only one directed link when mutual dependencies are asymmetric (Figure 2c). Changing to unidirectional interactions determined by the observed direction of asymmetry, as a surrogate of bidirectional mutual dependences, does not alter the relative manageabilities of different networks (Supplementary Information S2). Moreover, it confers an additional advantage for our purposes since it dramatically reduces the number of links in the network. This translates into a substantial reduction of the time and memory required for the computation of all possible maximum matchings in a network, particularly for large networks (see "Relative importance of species" subsection below).

#### Statistical analysis

Although understanding the variability of manageability across ecological networks is a useful result itself, we also wanted to test whether invasion status has 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 also 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 included the total number of species, plant richness, pollinators richness, the ratio of plants to pollinators richness, and the study site (as a two level factor). We assessed competing models by comparing the Akaike Information Criterion corrected for small sample sizes (AICc), and report results for the most parsimonious model.

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 has not been tested for in weighted ecological networks. We therefore compared the manageability of the empirical networks to networks generated by two null models which varied in terms of the constraints they impose. The first set was generated by maintaining each species' degree (its number of interactions) while allowing the number of visits per species to vary. The second set of random networks maintained each species' strength (its total sum of visits) while allowing their degrees to vary. Randomisations were generated using vegan 2.3-3 (Oksanen *et al.* 2016). After generating the randomized networks under these two schemes, we then calculated the mutual dependences and interaction asymmetries of each and determined their manageability using our maximum matching framework Finally, we calculated the average rank (akin to a p-value) of the manageability of each empirical network compared to the corresponding manageabilites of each set of 999 randomisations.

Beyond network structure, the dependency 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 manageability results above. We therefore performed an additional randomisation in which we kept the structure of network constant but randomised the direction of the interaction asymmetries. That is, we first calculated the asymmetries for each community and then shuffled the direction of the link between each pair of species. Similar as to the other null models, we calculated the average rank of the empirical manageability when compared to those of the randomisations.

### Relative importance of species

Our second key question is related to how species differ in their importance for driving 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 with which each species is deemed to be a superior node in the set of matchings that had a total weight greater or equal to 0.5 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 (mutual dependences and interaction asymmetries); however, the choice of this threshold had a negligible impact on the results (Supplementary Information S3).

Although the species importance calculated from mutual dependences contains full information, even in sparse networks, like those studied here, the number of maximal matchings increases exponentially with the number of links and nodes in a network. Unfortunately, this means that the large number of links in the most diverse communities rendered the computation unfeasible when we used mutual dependencies. Taking this limitation into account, we compared the relative network manageability obtained when using asymmetries to those found when using mutual dependencies to test if they gave consistent results. The comparison was performed for eleven of the twenty networks (those for which the number of matchings was smaller than 4 x 1010), using a paired Spearman correlation test, a weighted correlation coefficient *rw2* (which gives more weight to higher ranks; Pinto Da Costa *et al.* 2015), and a Jaccard similarity of the driver species in both approaches. All three approaches identified a high similarity in relative ranks. Consequently, we focused on the results when using the asymmetries rather than mutual dependencies when further investigating the factors that determine species' relative importance since this also allows us to obtain results for all 20 networks.

#### Statistical analysis

We then asked the question of whether some species-level structural properties can predict our estimates of species importance. We used a generalised linear mixed-effects model (with binomial error structure) with the relative importance as the response variable. 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); two measures of strength of association and dependence (visitation and dependency strength), as their distribution determines the extent of interspecific effects (Bascompte *et al.* 2006). In addition, we also included guild and invasive status 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). We lastly 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 & 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).

## Results

### Community manageabiity

All of the networks studied here 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 with the results obtained using the dependence asymmetry in which manageability ranged between 0.08 and 0.45 (mean 0.24; Spearman rank correlation 0.93, *p* < 0.001). In addition, we found that invaded communities were significantly more difficult to manage than uninvaded ones even when controlling for potential diversity effects (Figure 3). Out of the various covariates we explored—total number of species, plant richness, pollinator richness, and the ratio of plant to pollinator richness—only the ratio of plant to pollinator richness was retained in the final model as determined by the AICc (Table S4).

When exploring the effect of network structure itself, we observed that the manageability of empirical networks was, in general, not significantly different to the manageability of network randomisations that maintained the degree or the strength of individual species (Figure 4). However, when comparing the empirical network to randomisations that maintained the network structure but randomised only the direction of the asymmetries, we found that empirical networks showed a significant tendency to have smaller values of manageability.

### Relative importance of species

We found a strong agreement between the values of relative species' importance in the 11 networks for which we were able to calculate them using both mutual dependencies and asymmetries (Spearman's rank correlation ranged between *ρ* = [0.6, 0.78], median 0.69). Moreover, both approaches identified a highly similar set of driver species (Jaccard similarity *J* = [0.5, 1], median 0.67). Notably, we found that the agreement was stronger for highly ranked species than for lowly ranked species (mean *rw2* = 0.72 versus 0.59) when using the weighted rank correlation coefficient. Given the overall similarities, we concentrated on the relative rankings obtained using asymmetries in the following results.

Invasive species were driver species in every single network they were present, that is, they always had the highest relative ranking of species importance (Figure 5). Overall, plants showed significantly higher levels of importance than pollinators (Mann-Whitney-Wilcoxon test, *p* = 0.004). However, this difference can largely be 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 models that accounted at least 95% of the evidence based on AICc, we found that species' 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 had only a marginal effect on its relative importance.

## Discussion

Our results reveal that the structural differences associated with biotic invasions are reflected in a potential decrease in our ability to alter the state of the community post invasion. Furthermore, invasive mutualists were always driver species in the communities they invade. As driver species, they occupy a particularly dominant role in which changes on their abundance have the potential to propagate broadly trough the community and in turn affect the abundances of many other species.

At a community level, we demonstrate that the manageability of mutualistic networks is strongly governed by the asymmetric nature of mutual dependencies—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). Indeed, our empirical networks exhibit markedly lower levels of manageability compared to randomisations in which the visitation network was unchanged but where the observed patterns of dependence were broken. However, consistent with previous results (Liu *et al.* 2011), we show that the manageability of empirical networks was indistinguishable from that of networks with a random structure that maintained the degree or strength of each species in the community. Therefore, the asymmetries at the species level (specialization-generalization asymmetries) and the link level (interaction's dependence asymmetries) appear to be sufficiently constrained by the distribution of species degree and strength (Melián & Bascompte 2002). Generally speaking, this strong relationship between the asymmetric dependences and manageability might explain why invasive species reduce the manageability of their communities. Invasive species have been previously found to exacerbate the asymmetries in the network and ostensibly increase the stability of their community (Aizen *et al.* 2008; Bartomeus *et al.* 2008; Henriksson *et al.* 2016).

The changes in the asymmetries we found in the invaded networks are also reflected at a species level by the high relative importance of invasive species. However, 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 driver species 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 how important a species is for its community's dynamics.

Because of their effects on other species in the community, driver species might be natural candidates for management interventions. 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 as 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 useful for identifying conservation priorities, our approach is different to previous attempts to quantify species importance that concentrate on measures of centrality, position, co-extinction or uniqueness (Jordán *et al.* 2006; Jordán 2009; Lai *et al.* 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 abundance of a key species in turn affect the abundances of other members of the community (Paine 1969, 1995). However, while keystone species were traditionally identified by gauging how a community's population dynamics respond to a perturbation (Mills & Doak 1993), the driver species concept operates the other way round; namely, it uses the community 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, a purely experimental approach that identifies dynamically important species in a similar manner might be even more difficult to implement.

Overall, our investigation confirms the conclusions of previous studies that suggested that, in contrast to other types of complex systems, the structure of ecological networks renders them remarkably difficult to control (Liu *et al.* 2011; Ruths & Ruths 2014). In a hypothetical situation in which the goal were to regulate the abundances of all species in a pollination community, our results indeed suggest that we would need to directly intervene with the abundances of at least 40-90% of those species. Fully controlling an ecological community is no doubt an idealistaion, as designing and implementing 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 in one way or another.

In this study, we illustrate how a control-theoretic approach can be adopted when estimating the effect of invasions—a major driver of global change—on mutualistic communities. Notably, it can also be extended to understand the structural effects of other kind of perturbations and for systems governed by different types of interactions. Moreover, we see great potential by explicitly integrating control theory with dynamic models of species densities (Cornelius *et al.* 2013; Gibson *et al.* 2016). From an ecological perspective, this integration can provide even deeper insights into the relationship between controllability and species coexistence. It can also help identify potential trade-offs between persistence at the species and the community level. From a conservation perspective, the combined approach can shift our focus beyond the identification of ideal targets for intervention to design informed interventions that legitimately achieve restoration goals.

## 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, Matthew Hutchinson, and Marilia Gaiarsa for feedback in early stages of the project. 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.

## References

Aizen, M.A., Morales, C.L. & Morales, J.M. (2008). Invasive mutualists erode native pollination webs. *PLOS Biology*, 6, 0396–0403.

Albrecht, M., Padrón, B., Bartomeus, I. & Traveset, A. (2014). Consequences of plant invasions on compartmentalization and species’ roles in plant-pollinator networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 281, 20140773.

Astegiano, J., Massol, F., Vidal, M.M., Cheptou, P.-O. & Guimarães, P.R. (2015). The Robustness of Plant-Pollinator Assemblages: Linking Plant Interaction Patterns and Sensitivity to Pollinator Loss. *PLOS ONE*, 10, e0117243.

Ballantyne, G., Baldock, K.C.R. & Willmer, P.G. (2015). Constructing more informative plant-pollinator networks: visitation and pollen deposition networks in a heathland plant community. *Proceedings of the Royal Society B*, 282, 20151130.

Bartomeus, I., Vilà, M. & Santamaría, L. (2008). Contrasting effects of invasive plants in plant-pollinator networks. *Oecologia*, 155, 761–770.

Bartoń, K. (2016). MuMIn: Multi-Model Inference. *CRAN*.

Bascompte, J. & Stouffer, D.B. (2009). The assembly and disassembly of ecological networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 1781–7.

Bascompte, J., Jordano, P. & Olesen, J.M. (2006). Asymetric Coevolutionary Networks Facilitate Biodiversity Maintenance. *Science*, 312, 431–433.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software*, 67.

Baxter, C.V., Fausch, K.D., Murakami, M. & Chapman, P.L. (2004). Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology*, 85, 2656–2663.

Buckland, S.T., Burnham, K.P. & Augustin, N.H. (1997). Model Selection: An Integral Part of Inference. *Biometrics*, 53, 603–618.

Burnham, K.P. & Anderson, D.R. (2003). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Second. Springer, New York.

Cornelius, S.P., Kath, W.L. & Motter, A.E. (2013). Realistic control of network dynamics. *Nature Communications*, 4, 1942.

Csardi, G. & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems*, 1695, 1–9.

Dormann, C.F., Gruber, B. & Fründ, J. (2008). Introducing the bipartite Package: Analysing Ecological Networks. *R News*, 8, 8–11.

Ehrenfeld, J.G. (2010). Ecosystem Consequences of Biological Invasions. *Annual Review of Ecology, Evolution, and Systematics*, 41, 59–80.

Gibson, R.H., Knott, B., Eberlein, T. & Memmott, J. (2011). Sampling method influences the structure of plant-pollinator networks. *Oikos*, 120, 822–831.

Gibson, T.E., Bashan, A., Cao, H.-t., Weiss, S.T. & Liu, Y.-y. (2016). On the Origins and Control of Community Types in the Human Microbiome. *PLOS Computational Biology*, 12, e1004688.

Green, J.L., Hastings, A., Arzberger, P., Ayala, F.J., Cottingham, K.L. & Cuddington, K. *et al.* (2005). Complexity in Ecology and Conservation: Mathematical, Statistical, and Computational Challenges. *BioScience*, 55, 501–510.

Gutin, G. (2013). Independence and Cliques. In: *Handbook of graph theory* (ed. Zhang, P.). Chapman; Hall/CRC, pp. 475–489.

Henriksson, A., Wardle, D.A., Trygg, J., Diehl, S. & Englund, G. (2016). Strong invaders are strong defenders - implications for the resistance of invaded communities. *Ecology Letters*, 19, 487–494.

Isbell, F. & Loreau, M. (2013). Human impacts on minimum subsets of species critical for maintaining ecosystem structure. *Basic and Applied Ecology*, 14, 623–629.

Jordán, F. (2009). Keystone species and food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 1733–1741.

Jordán, F., Liu, W.-c. & Davis, A.J. (2006). Topological keystone species: measures of positional importance in food webs. *Oikos*, 112, 535–546.

Jørgensen, S.E., Mejer, H. & Nielsen, S.N. (1998). Ecosystem as self-organizing critical systems. *Ecological Modelling*, 111, 261–268.

Lai, S.-M., Liu, W.-C. & Jordan, F. (2012). On the centrality and uniqueness of species from the network perspective. *Biology Letters*, 8, 570–573.

Lever, J.J., Nes, E.H. van, Scheffer, M. & Bascompte, J. (2014). The sudden collapse of pollinator communities. *Ecology Letters*, 17, 350–359.

Levin, S. (1999). *Fragile Dominion*. Perseus, Cambridge, MA.

Liu, Y.-Y. & Barabási, A.-L. (2015). Control Principles of Complex Networks. *arXiv preprint*, 1508.05384, 1–61.

Liu, Y.-Y., Slotine, J.-J. & Barabási, A.-L. (2011). Controllability of complex networks. *Nature*, 473, 167–173.

Lopezaraiza-Mikel, M.E., Hayes, R.B., Whalley, M.R. & Memmott, J. (2007). The impact of an alien plant on a native plant-pollinator network: An experimental approach. *Ecology Letters*, 10, 539–550.

Lukacs, P.M., Burnham, K.P. & Anderson, D.R. (2010). Model selection bias and Freedman’s paradox. *Annals of the Institute of Statistical Mathematics*, 62, 117–125.

McDonald-Madden, E., Sabbadin, R., Game, E.T., Baxter, P.W.J., Chadès, I. & Possingham, H.P. (2016). Using food-web theory to conserve ecosystems. *Nature Communications*, 7, 10245.

Melián, C.J. & Bascompte, J. (2002). Complex networks: two ways to be robust? *Ecology Letters*, 5, 705–708.

Memmott, J., Waser, N.M. & Price, M.V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society B*, 271, 2605–2611.

Menge, B.A. (1995). Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs*, 65, 21.

Mills, L.S. & Doak, D.F. (1993). The Keystone-Species Concept in Ecology and Conservation. *BioScience*, 43, 219–224.

Montoya, M., Pimm, S.L. & Sole, R.V. (2006). Ecological networks and their fragility. *Nature*, 442, 259–264.

Ne’Eman, G., Jürgens, A., Newstrom-Lloyd, L., Potts, S.G. & Dafni, A. (2010). A framework for comparing pollinator performance: Effectiveness and efficiency. *Biological Reviews*, 85, 435–451.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R. & O’Hara, R.B. *et al.* (2016). *vegan: Community Ecology Package*.

Olesen, J.M., Eskildsen, L.I. & Venkatasamy, S. (2002). Invasion of pollination networks on oceanic islands: Importance of invader complexes and endemic super generalists. *Diversity and Distributions*, 8, 181–192.

Paine, R. (1995). A conversation on refinining the concept of keystone species. *Conservation Biology*, 9, 962–964.

Paine, R.T. (1969). A Note on Trophic Complexity and Community Stability. *The American Naturalist*, 103, 91.

Palacio, R.D., Valderrama-Ardila, C. & Kattan, G.H. (2016). Generalist Species Have a Central Role In a Highly Diverse Plant-Frugivore Network. *Biotropica*, 48, 349–355.

Pascual, M. & Dunne, J.A. (Eds.). (2005). *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford University Press, New York.

Pinto Da Costa, J., Roque, L.A. & Soares, C. (2015). The weighted rank correlation coefficient r2w in the case of ties. *Statistics & Probability Letters*, 99, 20–26.

Rodewald, A.D., Rohr, R.P., Fortuna, M.A. & Bascompte, J. (2015). Does removal of invasives restore ecological networks? An experimental approach. *Biological Invasions*, 2139–2146.

Ruths, J. & Ruths, D. (2014). Control profiles of complex networks. *Science*, 343, 1373–6.

Saavedra, S., Stouffer, D.B., Uzzi, B. & Bascompte, J. (2011). Strong contributors to network persistence are the most vulnerable to extinction. *Nature*, 478, 233–235.

Smith, A.M., Reinhardt Adams, C., Wiese, C. & Wilson, S.B. (2016). Re-vegetation with native species does not control the invasive Ruellia simplex in a floodplain forest in Florida, USA. *Applied Vegetation Science*, 19.

Solé, R.V. & Montoya, J.M. (2001). Complexity and fragility in ecological networks. *Proceedings of the Royal Society B*, 268, 2039–45.

Stouffer, D.B., Cirtwill, A.R. & Bascompte, J. (2014). How exotic plants integrate into pollination networks. *Journal of Ecology*, 102, 1442–1450.

Stouffer, D.B., Sales-Pardo, M., Sirer, M.I. & Bascompte, J. (2012). Evolutionary Conservation of Species’ Roles in Food Webs. *Science*, 335, 1489–1492.

Suding, K.N., Gross, K.L. & Houseman, G.R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution*, 19, 46–53.

Traveset, A., Heleno, R., Chamorro, S., Vargas, P., Mcmullen, C.K. & Nogales, M. *et al.* (2013). Invaders of pollination networks in the Galápagos Islands : emergence of novel communities. *Proceedings of the Royal Society B*, 280, 20123040.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11, 1351–1363.

Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation*, 143, 2270–2279.

Vázquez, D.P. & Aizen, M.A. (2004). Asymmetric specialization: a pervasive feature of plant-pollinator interactions. *Ecology*, 85, 1251–1257.

Vázquez, D.P., Morris, W.F. & Jordano, P. (2005). Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology Letters*, 8, 1088–1094.

Vilà, M., Bartomeus, I., Dietzsch, A.C., Petanidou, T., Steffan-Dewenter, I. & Stout, J.C. *et al.* (2009). Invasive plant integration into native plant-pollinator networks across Europe. *Proceedings of the Royal Society B*, 276, 3887–3893.

West, D. (2001). *Introduction to graph theory*. Prentice Hall, Upper Saddle River.