

# STRUCTURAL CONTROLABILITY OF POLLINATION NETWORKS

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## 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 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.

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 dynamics of other species in the community. .

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