

Attachment 1

## STRUCTURAL CONTROLABILITY OF POLLINATION NETWORKS

E. Fernando Cagua, Kate Wootton, Anna J. Voinopol Sassu, and  
Daniel B. Stouffer

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

### **1      Introduction**

2      Ecological communities are formed by the interconnection of several species.  
3      Therefore, changes in the abundances of one species can potentially alter the  
4      abundances of the species they interact with. For instance, in a classic example  
5      of ecosystem cascades, a reduction on the abundance of sea otters, an important  
6      predator or sea urchins, can drive a dramatic reduction on kelp abundances be-  
7      cause the sea urchins that consume kelp are released from predation. It has been  
8      long established that some species, like the sea otter, have a disproportionate  
9      large effect in their environment relative to their abundance.

10     In several ecosystems the relative importance of species have been identified  
11    based on empirical observations of long term dynamics. However, in less stud-  
12    ied, highly diverse, or where the "keystone" role is shared by several species, it  
13    can be challenging to determine which is the set of species that influence the  
14    most the ecosystem dynamics. Alternative approaches that recognize a contin-  
15    uum of importance and that are less dependent on empirical observations have  
16    also been developed. Some of them are based on metrics that evaluate their  
17    position in the food web or on mass balance models of functional groups. Nev-  
18    ertheless, these approaches are conceptually limited to trophic interactions and

19 in general ignore the structural mechanisms that allow or prevent the spread of  
20 perturbations in the ecosystem.

21 From a systems perspective, perturbations like over-exploitation, eutrophication  
22 or global warming are equivalent to management actions like culling,  
23 no-take areas or captive rearing in the sense that they have the potential to  
24 modify the abundances of one or several species in the ecosystem. Therefore  
25 identifying these key species is crucial not only to predict how these perturba-  
26 tions will spread through the community but also to guide effective conservation  
27 efforts.

28 Recent work on the control of complex systems suggest that in principle it  
29 is possible to alter any ecological community's composition, by modifying the  
30 abundances of just some key species (Isbell and Loreau 2013; Cornelius, Kath,  
31 and Motter 2013). Here, we apply these theories to estimate the controllability  
32 of different ecological communities and to find driver species: species, that due  
33 to the structural characteristics of their interactions are more likely to drive the  
34 dynamics of the community.

35 Invasive species have been shown to have a disproportionate effect on the  
36 structure of pollination communities. Influencing for example the strength of  
37 species interactions, and the degree of network nestedness and connectivity (Jens  
38 M. Olesen, Eskildsen, and Venkatasamy 2002; Aizen, C. L. Morales, and J. M.  
39 Morales 2008; Bartomeus, Vilà, and Santamaría 2008; Vilà et al. 2009; Traveset  
40 et al. 2013). However whether this influence is translated into a driver role  
41 has not been tested. Here we use plant pollinator communities to investigate  
42 the number of species that should be managed to control population dynamics  
43 of the whole community, the characteristics that determine whether a species  
44 should be managed or not and how invasive species fit.

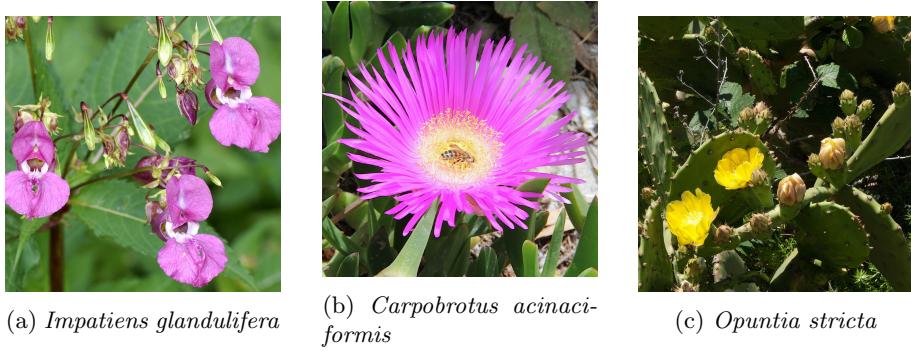


Figure 1: Invasive species present in the studied pollination communities (photographs by Udo Schmidt, Peter Mansfeld, and Tony Rodd).

45 Methods

To investigate the dynamic controllability of pollination networks, we used ten paired plants-pollinator communities. Each pair was composed by a community invaded by a plant and a community free of the invasive species. Weighted visitation networks were constructed from previously published visitation data collected from pollination communities in Bristol, Great Britain (Lopezaraiza-Mikel et al. 2007) and the National Cap de Creus in Northeastern Spain (Barbomeus, Vilà, and Santamaría 2008). The four British uninvaded communities the non-invaded plots were obtained by experimentally removing the invasive species *Impatiens glandulifera* (Figure 1a). Contrastingly, Spanish uninvaded communities were obtained from plots that were not been colonised by the invasive species *Carpobrotus edulis* or *Opuntia stricta* (Figure 1b, c). In each of the networks we calculated the minimum number of driver species—species that need to be managed in order to gain full control of the community.

We first assigned a direction to each link between plants and pollinators given by the direction of dependency. For each link between a plant and its pollinator we quantified the level of dependency of the plant on the pollinator and vice versa (Bascompte, Jordano, and Jens M Olesen 2006). The link points to the plant if the its dependency on the pollinator is larger than the pollinator's

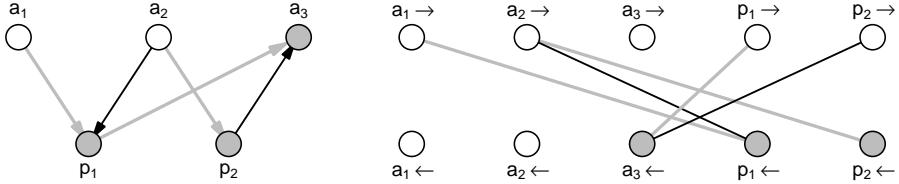


Figure 2: On the left a simple pollination network; the direction of the arrows indicates the direction of the largest dependency between species pairs. On the right the representation of the network used to calculate the maximum matching (in grey). Matched species, i.e. those whose dynamic could be “controlled” by another species are shown in blue. Note that the maximum matching is not necessarily unique.

dependency on the plant. The dependency of plant  $i$  on pollinator  $j$  is the ratio between the visits coming from pollinator  $j$  and all pollinator visits to plant  $i$ . The dependency of pollinator  $j$  on plant  $i$  is the ratio of the visits by pollinator  $j$  to plant  $i$  and all visits of pollinator  $j$ .

In a directed network, a matching is a subset of links in which no two links share a common starting species or a common ending species. A species is matched if it is an ending node of an link in the matching. Otherwise, it is unmatched. It has been shown that the number of driver species can be calculated by counting the number of unmatched nodes in the directed graph representation of the pollination network (Liu, Slotine, and Barabási 2011). We then found a maximum in the an alternative bipartite representation of the pollination network (Csardi and Nepusz 2006) (Figure 2).

We calculated dependencies based on visitation frequency, which has been shown to be an appropriate surrogate of the inter-specific effects (Bascompte, Jordano, and Jens M Olesen 2006; Vázquez, Morris, and Jordano 2005). However, because the degree distribution, and ultimately the number of driver species, can be affected by the sampling method (Blüthgen 2010) we compared the number of driver species in a pollination community in which both visitation frequency and effectiveness were measured (Ballantyne, Baldock, and Willmer 2015).

84 To quantify to what extent the number of driver species is characteristic  
85 of the structure of pollination networks we compared them against a set of random  
86 null-models. A set of null models were based on network randomisations that  
87 maintained the degree of plants, pollinators, and both plants and pollinators. To  
88 analyse the effects of the chosen directionality, we devised a null model in which  
89 we randomised the visitation patterns and re-calculated the new dependencies.  
90 In all cases we computed 999 randomisations.

91 We quantified the relative importance of each species for network dynamics.  
92 To do this, we counted the number of times a particular species was a driver  
93 species across all possible maximum matchings in the pollination network. The  
94 number of maximum matchings were found by generating the line graph of the  
95 alternative bipartite network representation ([Figure 2](#)), and then enumerating  
96 the maximal cliques in the complement of the line graph (Csardi and Nepusz  
97 [2006](#)).

98 Finally, we tackled the question whether some structural properties can pre-  
99 dict the relative importance of driver species. Here, we regressed the impor-  
100 tance of each species against measures of centrality (degree, betweenness), mea-  
101 sures related to network robustness (contribution to nestedness) and measures  
102 of strength of association (visitation levels).

## 103 Preliminary results

104 To date only data from the National Cap de Creus in Northeastern Spain has  
105 been analysed. We found that if we were to control the dynamics of the whole  
106 community, we would need to control between 55 and 75% of the species in the  
107 community. The proportion of driver species did was not significantly different  
108 between invaded and uninvaded ecosystems.

109 Empirical pollination networks to randomisations have need significantly  
110 more driver species than randomisations that maintain the number of inter-

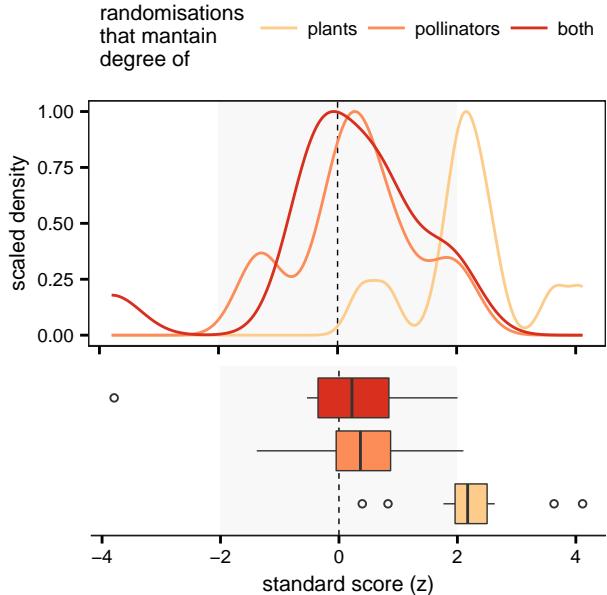


Figure 3: Difference between the number of driver species in the empirical pollination networks versus randomisations of the same networks. The unshaded area ( $z < -2, z > 2$ ) suggest a significant difference at a significance level of  $\alpha = 0.05$ .

111 acting species per plants. However when the number of interacting species is  
 112 maintained in pollinators or in all species, the difference disappear (Figure 3).  
 113 This suggest that the number of driver species is determined by the degree dis-  
 114 tribution of the species, in particular pollinators. This is consistent to previous  
 115 findings that highlight the influence of the degree distribution on the controlabil-  
 116 ity of complex networks (Liu, Slotine, and Barabási 2011; Benavides, Diwekar,  
 117 and Cabezas 2015).

118 However, when we compared the empirical networks to randomisations that  
 119 maintain the network structure but shuffle the directionality of the dependency,  
 120 we found that empirical networks need substantially more driver species than the  
 121 random counterpart (Figure 4). This highlights the importance of asymmetries  
 122 in structuring pollination networks.

123 Not all species have the same importance for network control. Pollinators

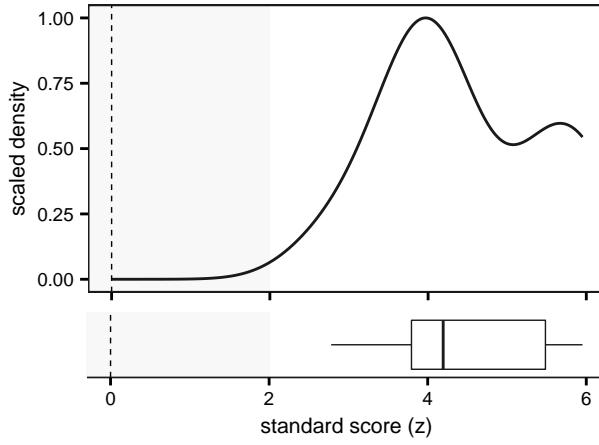


Figure 4: Difference between number of driver species in the empirical networks versus randomisations of the dependencies in the same networks. The unshaded area ( $z > 2$ ) suggest a significant difference at a significance level of  $\alpha = 0.05$ .

124 in general seem to have a moderate-high role on driving the dynamics of other  
 125 species. Plants on the other hand seem to be a skewed distribution, with some  
 126 species having a very low and some species having a very high relative impor-  
 127 tance (Figure 5).

128 When looking at the relative importance of invasive species we found that,  
 129 in all of the six analysed networks, they all have the maximum importance.  
 130 They are certainly not unique in this regard, but it is remarkable that invasive

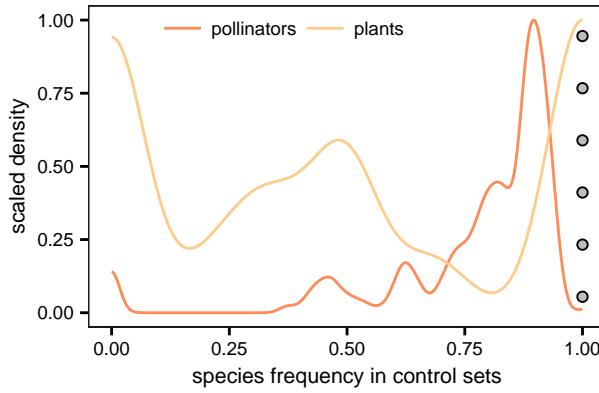


Figure 5: Distribution of the relative frequency a species is present in the set of driver species. Invasive species are depicted as grey points.

131 species integrate this way in the community.

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141 **References**

- 142 Aizen, Marcelo A, Carolina L Morales, and Juan M Morales (2008). “Invasive  
143 mutualists erode native pollination webs”. In: *PLoS Biology* 6.2, pp. 0396–  
144 0403. DOI: [10.1371/journal.pbio.0060031](https://doi.org/10.1371/journal.pbio.0060031).
- 145 Ballantyne, G, Katherine C R Baldock, and P G Willmer (2015). “Constructing  
146 more informative plant-pollinator networks: visitation and pollen deposition  
147 networks in a heathland plant community”. In: *Proceedings of the Royal  
148 Society B* 282.1814, p. 20151130. DOI: [10.1098/rspb.2015.1130](https://doi.org/10.1098/rspb.2015.1130).
- 149 Bartomeus, Ignasi, Montserrat Vilà, and Luís Santamaría (2008). “Contrasting  
150 effects of invasive plants in plant-pollinator networks”. In: *Oecologia* 155.4,  
151 pp. 761–770. DOI: [10.1007/s00442-007-0946-1](https://doi.org/10.1007/s00442-007-0946-1).
- 152 Bascompte, Jordi, Pedro Jordano, and Jens M Olesen (2006). “Asymmetric Coevo-  
153 lutionary Networks Facilitate Biodiversity Maintenance”. In: *Science* 312.April,  
154 pp. 431–433. DOI: [10.1126/science.1123412](https://doi.org/10.1126/science.1123412).

- 155 Benavides, Pahola T, Urmila Diwekar, and Heriberto Cabezas (2015). “Controllability of complex networks for sustainable system dynamics”. In: *Journal of Complex Networks* 3.4, pp. 566–583. DOI: [10.1093/comnet/cnu051](https://doi.org/10.1093/comnet/cnu051).
- 156
- 157
- 158 Blüthgen, Nico (2010). “Why network analysis is often disconnected from community ecology: A critique and an ecologist’s guide”. In: *Basic and Applied Ecology* 11.3, pp. 185–195. DOI: [10.1016/j.baae.2010.01.001](https://doi.org/10.1016/j.baae.2010.01.001).
- 159
- 160
- 161 Cornelius, Sean P, William L Kath, and Adilson E Motter (2013). “Realistic control of network dynamics”. In: *Nature Communications* 4, p. 1942. DOI: [10.1038/ncomms2939](https://doi.org/10.1038/ncomms2939). arXiv: [1307.0015](https://arxiv.org/abs/1307.0015).
- 162
- 163
- 164 Csardi, G and T Nepusz (2006). “The igraph software package for complex network research”. In: *International Journal of Complex Systems* Complex Sy.June, p. 1695. DOI: [10.1109/ICCSN.2010.34](https://doi.org/10.1109/ICCSN.2010.34).
- 165
- 166
- 167 Isbell, Forest and Michel Loreau (2013). “Human impacts on minimum subsets of species critical for maintaining ecosystem structure”. In: *Basic and Applied Ecology* 14.8, pp. 623–629. DOI: [10.1016/j.baae.2013.09.001](https://doi.org/10.1016/j.baae.2013.09.001).
- 168
- 169
- 170 Liu, Yang-Yu, Jean-Jacques Slotine, and Albert-László Barabási (2011). “Controllability of complex networks.” In: *Nature* 473.7346, pp. 167–173. DOI: [10.1038/nature10011](https://doi.org/10.1038/nature10011).
- 171
- 172
- 173 Lopezaraiza-Mikel, Martha E. et al. (2007). “The impact of an alien plant on a native plant-pollinator network: An experimental approach”. In: *Ecology Letters* 10.7, pp. 539–550. DOI: [10.1111/j.1461-0248.2007.01055.x](https://doi.org/10.1111/j.1461-0248.2007.01055.x).
- 174
- 175
- 176 Olesen, Jens M., Louise I. Eskildsen, and Shadila Venkatasamy (2002). “Invasion of pollination networks on oceanic islands: Importance of invader complexes and endemic super generalists”. In: *Diversity and Distributions* 8.3, pp. 181–192. DOI: [10.1046/j.1472-4642.2002.00148.x](https://doi.org/10.1046/j.1472-4642.2002.00148.x).
- 177
- 178
- 179
- 180 Traveset, Anna et al. (2013). “Invaders of pollination networks in the Galápagos Islands : emergence of novel communities”. In: *Proceedings of the Royal Society B* 280.iii, p. 20123040. DOI: [10.1098/rspb.2012.3040](https://doi.org/10.1098/rspb.2012.3040).
- 181
- 182
- 183 Vázquez, Diego P., William F. Morris, and Pedro Jordano (2005). “Interaction frequency as a surrogate for the total effect of animal mutualists on plants”.
- 184

- 185        In: *Ecology Letters* 8.10, pp. 1088–1094. DOI: [10.1111/j.1461-0248.2005.00810.x](https://doi.org/10.1111/j.1461-0248.2005.00810.x).
- 186        Vilà, Montserrat et al. (2009). “Invasive plant integration into native plant-
- 187        pollinator networks across Europe.” In: *Proceedings of the Royal Society B*
- 188        276.1674, pp. 3887–3893. DOI: [10.1098/rspb.2009.1076](https://doi.org/10.1098/rspb.2009.1076).