Structural controllability of ecological networks

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Abstract

1. Background

2. Methods

3. Results

4. Synthesis

Keywords: ASD

Introduction

A major goal in ecology is to understand the roles played by different species in the biotic environment. Within community ecology, a complex-systems approach has led to the development of a variety analytical and simulation tools with which to compare and contrast the roles of species embedded in a network of interactions (J. Bascompte & Stouffer, 2009; Coux, Rader, Bartomeus, & Tylianakis, 2016; Guimerà & Amaral, 2005; Stouffer, Sales-Pardo, Sirer, & Bascompte, 2012). A particularly relevant dimension of any species' role is its ability to alter the abundance of other species and the state of the community—since changes of this nature can have knock-on effects on ecosystem function, diversity, processes, and services. This ability is sometimes referred to as a species' "keystoneness" (Mills & Doak, 1993).

A significant proportion of the network tools used to estimate species roles in this context rely on the calculation of a species' centrality—a relative ranking of its positional importance that stems from social network research (Friedkin, 1991). Generally speaking, central species tend to be better connected and consequently are more likely to participate in the network's food chains. Because species that participate in more chains are assumed to be more likely to affect the abundance of other species, centrality metrics have often been used to identify keystone species in the community (Jordán, Benedek, & Podani, 2007). Centrality metrics have been shown to be useful tools to rank species in regards to their potential to alter the abundances of other species; especially when estimating secondary extinctions that may follow the loss of a species (Dunne, Williams, & Martinez, 2002; Kaiser-Bunbury, Muff, Memmott, Müller, & Caflisch, 2010).

Despite being conceptually intuitive, the relationship between centrality and the state of the community is largely phenomenological. On one hand, dramatic changes in ecosystem functioning can also occur without complete removal of a species. On the other, we are often interested in a *specific* state of the community that might be desirable to attain (or preserve) because of its biodiversity, resilience, functioning, or the

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services it provides. In these cases, it might not enough to understand which species may cause *any* change in the community. Rather we need to understand first, how the structure of the network can be harnessed to achieve the desired state and which species may play the largest role in this process. When the state of a community is underpinned by more than a single species and we move beyond single-species removals, we expect the usefulness of centrality to diminish. As a result, community ecology could arguably benefit from an alternative, perhaps more mechanistically-grounded, approach to understand how species affect each other's abundance.

Species abundances (and consequently the state of the community) are influenced by both their interactions, the specific dynamics of these interactions and the mechanisms of self-regulation. However, community and population dynamics can be modelled in innumerable ways, and empirical support for one versus another is often still ambiguous. The alternative approach should, therefore, ideally acknowledge ecosystem dynamics, but without being overly dependent on the particular choices of how they are characterised. Among the various possibilities, *control theory* appears to be a strong candidate (Isbell & Loreau, 2013). Control theory is a widely-studied branch of engineering used to determine and supervise the behaviour of dynamical systems (A. E. Motter, 2015). It is inherently designed to deal with system feedbacks and its application has recently been expanded to complex networks (Lin, 1974; Liu & Barabási, 2016). In concordance with long-standing ecological questions, advances in this field have established a clear link between the structure of the network and the way nodes affect each other. Unlike centrality indices, however, this link is not based on a priori assumptions between network metrics and keystoneness but is instead based on well-established advances in both dynamical and complex-systems theory.

At its fundamental level, control theory first determines whether a system is controllable or not; that is, it asks if a system can be driven to a desired state within a finite amount of time. Although the controllability of a network is a whole-system property, it has been recently shown that asking for the controllability of a complex-system is equivalent to finding a particular set of nodes: the set with which is possible to control the state of the whole network (Liu & Barabási, 2016). Notably, control theory is consistent with the observation that to change the state of a network, more than a ranking, we need a set of nodes. Importantly, this set of nodes is not always unique for a given network. This implies that an examination of the distinct sets provides a means to connect nodes with its *general* ability to modify the system to which they belong.

Here, we apply methods from control theory to a particular ecological problem and show how it can be used to gain insight into the role of species in an ecological network. Specifically, we outline the approach using a set of ten pairs of uninvaded and invaded plant-pollinator communities. We use invaded communities because there is strong empirical evidence showing that invasive species play an important role shaping the abundances of other species, something which is particularly true in these ten networks

(Bartomeus, Vilà, & Santamaría, 2008; Lopezaraiza–Mikel, Hayes, Whalley, & Memmott, 2007). This choice thus offers us an opportunity to explicitly contrast our theoretical observations with empirical evidence. Empirical observations indicate that steering the state of some communities—for example during ecosystem restoration or invasive species removal—can be a very difficult task (Woodford et al., 2016). Therefore, with these networks, we first ask whether there are differences between the controllability of invaded and uninvaded networks. We then expand existing methods from control theory to effectively link the *controllability* of a network with the role of particular species. We ask—from a control-theoretic perspective—whether there are key differences between species in the role they play at driving the state of the community and explore the ecological factors related to these differences. This allows us to identify species that might be critical for network control and show that they have a larger than expected impact on the structural stability of the community. Finally, we compare the proposed approach to current methods based on species centrality and show how these methods are indeed valuable but ultimately paint a limited picture in regards to the "keystoneness" of a species and its role at supporting the diversity of its community.

Materials and methods

We used ten paired pollination communities to apply the control-theoretic approach. Each community pair was composed of a community invaded by a plant and a community free of the invasive species. Four pairs correspond to natural or semi-natural vegetation communities in the city of Bristol, UK (Lopezaraiza–Mikel et al., 2007). These communities are comprised of 19–87 species (mean 55), and non-invaded plots were obtained by experimentally removing all the flowers of the invasive species *Impatients grandulifera*. The other six pairs were obtained from lower diversity Mediterranean shrublands in Cap de Creus National Park, Spain (Bartomeus et al., 2008). These communities are comprised of 30–57 species (mean 38); in contrast to the above, 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 these communities was defined by the pollinator visitation frequency, which has been shown to be an appropriate surrogate for interspecific effects in pollination networks (J. Bascompte, Jordano, & Olesen, 2006; Diego P. Vázquez, Morris, & Jordano, 2005). Full details about the empirical networks can be found in the Supporting Information Section S1.

The first step in applying methods of control theory is to construct a directed network that is able to provide an indication of the extent to which species affect each other's abundance. In some ecological networks, establishing the directionality can be relatively straightforward, for example when links represent biomass transfer or energy flow (Isbell & Loreau, 2013). In pollination networks, however, this directionality

is less obvious as both species can, in theory, benefit from the interaction. We overcome that obstacle by noting that the extent to which species i affects species j relative to the extent to which j affects i can be summarised by the interaction asymmetry (J. Bascompte et al., 2006). This asymmetry is given by

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

where the dependence of plant i on pollinator j, d_{ij}, is the proportion of the visits from pollinator j compared to all pollinator visits to plant i. Previous research has shown that mutualistic interactions are often highly asymmetric in natural communities; in other words, if a plant species is largely dependent on a pollinator species, that pollinator tends to depend rather weakly on the plant (and vice versa). We, therefore, create a directed link from species i to species j when $d_{ij} - d_{ji} \geq 0$ to establish the most likely direction of control between a species pair (Figure 1a). Sometimes there is no observed asymmetry between species pairs ($d_{ij} = d_{ji}$), and we cannot infer a dominant direction of control. When this occurs, we deem both species to be equally likely to affect each other and form a reciprocal interaction between them (a link from i to j and another from j to i). By basing the direction of the links on the asymmetry of their dependence, we are able to generate a network that is consistent with the dynamics of the community while satisfying the requirements of structural controllability. That allows us to calculate the controllability of the networks and investigate whether there are differences between invaded and uninvaded communities.

Controllability

A system is said to be controllable if it is possible to steer it from an initial to an arbitrary final state within finite time (Kalman, 1963). A simple version of such a system can be described by $\frac{dx}{dt} = Ax + Bu(t)$, where the change of its state over time ($\frac{dx}{dt}$) depends on its current state x (for example, the species' abundances), an external time-varying input $u(t)$ (the control signal), and two matrices A and B, which encode information about the network structure and how species respond to external inputs, respectively. In classic control theory, determining wether this system is controllable can be achieved by checking that its controllability matrix $R = \begin{bmatrix} B & AB & A^2B & ... & A^{n-1}B \end{bmatrix}$ has full rank. In complex systems, however, employing this rank condition, or numerical approximations of it, is infeasible because it is hard to fully parameterize A and B (either because the weight of the links changes over time or because they are difficult to measure). Here we use an approach based on the structural controllability theorem (Lin, 1974), which assumes that we are confident about which elements of A and B have either non-zero or zero values (there is an interaction or not), but that we less sure about the precise magnitude of the non-zero values. Using this structural approach we can find out the controllability of a system for every non-zero realisations of the parameters. An intuitive way to understand structural controllability is by looking
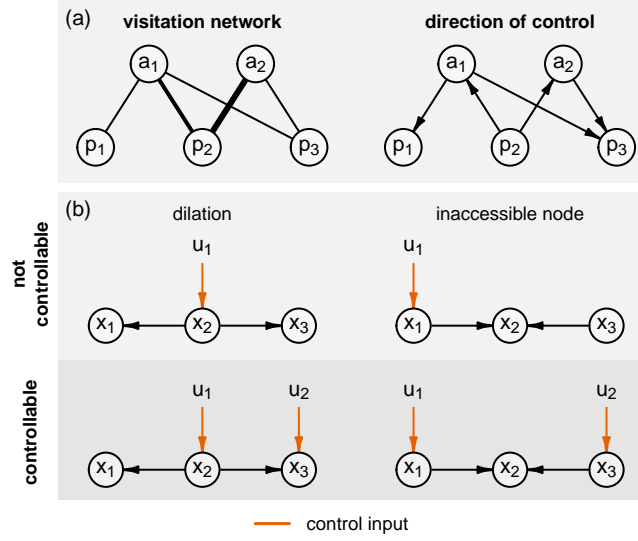
Figure 1: The direction of control and controllability conditions. (a) To establish the direction of control we start with a weighted visitation network (on the left). In this network, the width of the links corresponds to the frequency of visitation between animals a_i and plants p_i, with wider links indicating more visits. Plant p_1 is visited exclusively by a_1 but p_1 represents only a small fraction of the floral resources of a_1. Therefore the population of p_1 is more likely to be affected by a_1 than vice-versa. We represent this with a directed link from a_1 to p_1 (right). The direction of control between all other species pairs can be similarly determined by inspecting the difference between their relative dependences. (b) Once we have established the directions of control we can determine whether the network is controllable or not. A system defined by a directed network (with state nodes x_i; species populations in an ecological context) and external control inputs (nodes u_i, orange links) is structurally controllable if it satisfies two conditions: it has no dilations (expansions in the network) and no inaccessible nodes. The system on the top left is not controllable because there is a dilation in which node x_2 is being used to control two nodes simultaneously, in other words, there are fewer superiors (x_2) than subordinates (x_1 and x_3). The network in the top right is not controllable because node x_3 is inaccessible for the only input node u_1 in the system. Both systems can be made controllable by adding an extra input node (top).

at its graphical interpretation: from a topological perspective a network is structurally controllable if there are no inaccessible nodes—nodes without incoming links—or dilations—*expansions* of the network (Figure 1b; Supporting Information Section S2).

We are often able to estimate A in ecological networks, as this matrix represents the interactions between species. Part of the control problem resides in estimating a supportable estimation of B, which represents the links between external inputs and species. Naively, any ecological community (and any system for that matter) could be controlled if we control the state of every species independently, but such an approach is typically impractical. Here, we are interested in finding a minimum driver node-set (effectively finding B) with which to make the system controllable. The brute-force search for this minimum driver node-set is computationally prohibitive for most networks as it involves the evaluation of 2^N different controllability matrices. We therefore instead employ a recently-developed approach that shows that the control problem of finding the minimum driver node-set can be mapped into a graph-theoretic problem: maximum matching (Liu & Barabási, 2016; Liu, Slotine, & Barabási, 2011).

Maximum-matching is a widely studied topic in graph theory and is commonly used in multiple applications, ranging from dating apps and wireless communications to organ transplant allocation and peer-to-peer file sharing. A matching in an unweighted directed graph is defined as a set of links that do not share a common start or end nodes; the largest possible matching is called a maximum matching. For example, in a network composed by jobs and job applicants, a matching is any pairing between applicants and positions that satisfies one basic constraint: an applicant can be assigned to at most one position and vice versa. Consequently, a maximum matching is an optimal pairing, one that maximises the number of applicants with jobs and the number of positions filled. Admittedly, the link between matchings and structural controllability may appear far from straightforward. The key is to note that the fundamental conditions of structural controllability imply that there is a one-to-one relationship between *superior* and *subordinate* nodes just like the one-to-one relationship between jobs and applicants (Figure 1b, bottom left). We thus use the maximum-matching algorithm to find an optimal pairing of superior and subordinate nodes in a manner consistent with the controllability conditions (Supporting Information Section S3.1). Given the result, we can further decompose the matching into a set of paths that reveal how a control signal can flow across the links in a network to reach every node that composes it. As recently shown (Liu et al., 2011), the minimum driver node-set—those to which an external control input should be applied to make the system controllable—corresponds exactly to the *unmatched* nodes in the network (Figure 2).
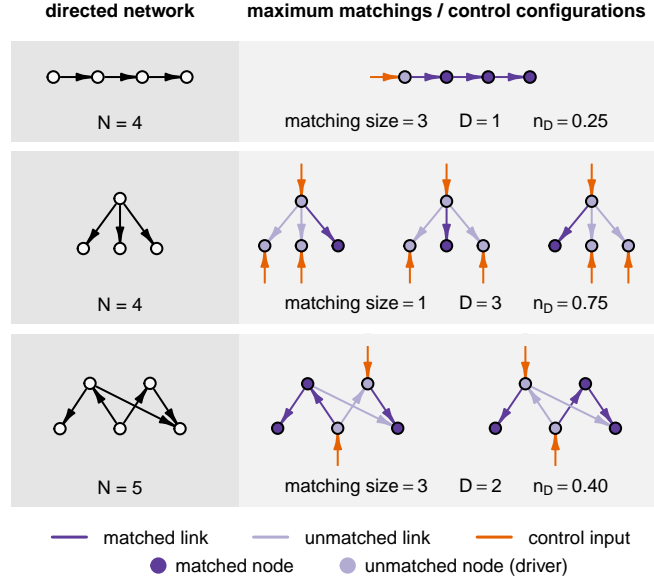
Figure 2: Maximum matchings and control configurations. In directed networks, a maximum matching is the largest possible set of links that do not share start or end nodes (dark purple). Maximum matchings are not necessarily unique, instead, each of them is related to a possible minimum driver node-set in the network (the nodes to which an external control input, in orange, should be applied in order to ensure controllability). The size of the minimum driver node-set D corresponds exactly to the number of unmatched nodes (the number of nodes in the network N minus the matching size). To account for network size, we use the size of the minimum driver node-set relative to the total number of nodes $n_D = D/N$ as a measure of the extent to which the network structure can be harnessed to control the system.

Differences between invaded and uninvaded networks

Our first ecological objective is to investigate whether the controllability of a community is associated with invasion status or not. Finding out exactly how difficult it is to control a network depends strongly on the particularities of the desired control trajectory as well as the dynamical relationship between nodes. However, we are interested in understanding the controllability of a network in a more general sense, such that it can be applied even when the precise control scenario is known only incompletely. To this end, we chose an indicator that follows directly from our approach: the size of the minimum driver node-set. This simple metric provides a general indication of how difficult controlling a network might be, as systems that require a large number of external inputs to be fully controlled are intuitively more difficult or costly to manage. For instance, achieving full control in a "network" in which species do not interact at all is relatively more difficult as we would require an intervention for every single species. Conversely, the structure of a linear trophic chain can be harnessed to achieve full control using just one intervention targeted the top species; the control signal would then cascade through the trophic levels and reach other species in the community. Specifically, drawing from the structural-controllability literature, we use the size of the minimum driver node-set relative to the total number of species $n_D = \frac{D}{N}$ as a measure of the *controllability* of a network—the extent to which the network structure can be harnessed to control the community. In an ecological context, external inputs can be thought of as management interventions that

modify the abundance of a particular species.

After finding the minimum driver node-set in each of our networks, we wanted to test whether invasion status or other predictors are correlated to controllability. We, therefore, use a set of generalised linear models (with binomial error structure). The response variable was the size of the minimum driver node-set n_D of the twenty empirical networks (ten invaded and ten uninvaded) and we included invasion status as a predictor. We also include the network connectance, the network nestedness (NODF), the number of species (since one might naively expect to see a negative relationship between richness and controllability; Menge, 1995), the network asymmetry (an indication of the balance between plant and pollinator diversity), and the interaction strength asymmetry (the asymmetry on the dependences between trophic levels; N. Blüthgen, Menzel, Hovestadt, Fiala, & Blüthgen, 2007). Models were compared using the Akaike Information Criterion for small sample sizes (AICc).

In addition, we also explored whether real networks differ in their architecture from random ones in a concerted way that could impact these results. Specifically, we used two null models each with 99 randomisations per network. In the first, we followed Diego P Vázquez et al. (2007) and maintained the connectance of the network but randomised the visits across species such that the relative probabilities of interactions were maintained. We then calculated the direction of control and the corresponding size of the minimum driver node-set, n_D. For the second null model, we used the empirical directed network and randomly shuffled the direction of control between a species pair.

Species roles

Our second key question is related to how species differ in their ability to drive the population dynamics of the community. Ecologically, these differences are relevant because resources and data are limited, and therefore full control is unfeasible. While calculating the size of the minimum drive node-set can measure the controllability of an ecological community, it does not provide information about the roles that particular species play.

To answer this question, we harness the fact there may be multiple maximum matchings for a given network, and each of these maximum matchings indicates a unique combination of species with which is possible to control the network. Some species belong to these combinations more often than others. We call this property a species control capacity, ϕ. The higher a species control capacity, the higher the likelihood that they would need to be directly managed to change (or maintain) the ecological state of their communities. Therefore a species' control capacity is an estimation of their relative importance at driving the state of the community (Jia & Barabási, 2013).

To calculate a species control capacity ϕ, we need to enumerate all possible maximum matchings

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(Supporting Information Section S3.2). However, enumerating all maximum matchings is extremely expensive from a computational perspective—a network with a couple dozen species has several hundred million unique maximum matchings. To solve this problem, we employ a recently-developed algorithm that reveals the control correlations between the nodes in the graph using considerably less computational resources (Zhang, Lv, & Pu, 2016). Using this algorithm, we are able to identify species that are possible control inputs—those that belong to the minimum driver node-set in at least one of the possible control configurations. One of the original contributions of our work is to extend this algorithm such that it is possible to calculate a highly accurate approximation of the control capacity ϕ_i of every species in the network (Supporting Information Section S3.3). In the networks that contained reciprocal links (because there was no asymmetry in the dependences of a species pair), we averaged a species' control capacity ϕ across every possible "non-reciprocal" version of the network (Supporting Information Section S3.4).

We then examined how species-level properties were related to control capacity using a set of generalised linear models with binomial error structure. As explanatory variables, we included five variables. First, the species contribution to nestedness, which has been proposed as a key feature that promotes stability and robustness in mutualistic networks (S. Saavedra, Stouffer, Uzzi, & Bascompte, 2011). Second, the species strength (the sum of a species' visits), which quantifies the strength of a species associations and is indirectly related to its abundance (Poisot, Canard, Mouquet, & Hochberg, 2012). Third, the direction of asymmetry which quantifies the net balance in dependencies, this is it indicates if a species affects other species more than what they affect it or not (Diego P Vázquez et al., 2007). Fourth, the species degree in order to account for the centrality of a species. Finally, we included a categorical variable for the species trophic level (plant or pollinator) and an interaction term between trophic level and the previous four variables. To facilitate comparison between predictors, degree and visitation strength were log-transformed and all four continuous variables were scaled to have a mean of zero and a standard deviation of one.

To identify the models that were best supported by the data we first determined the most parsimonious random structure using the AICc. The relative importance of variables was then assessed by looking at both their effect sizes in the top-ranked models and the cumulative weight of the models in which they are present.

Some species have a control capacity $\phi = 1$. These species are critical to controlling community because they are part of the minimum driver node-set in every control scenario. In other words, it is not possible to drive the state of the community to a desired state without directly managing the abundance of these species. We anticipate that these species have a disproportionally large impact on the community dynamics. Therefore, we determined the critical species in each of the networks and investigated whether they have a larger than average impact on the stable coexistence of species in the community. This

property of promoting stable coexistence is called structural stability (R. P. Rohr, Saavedra, & Bascompte, 2014). Mathematically it is denoted by the letter Ω and represents the size of the parameter space (growth rates, carrying capacities) under which all species can sustain positive abundances (S. Saavedra, Rohr, Olesen, & Bascompte, 2016). The contribution of species i to stable coexistence, can be estimated by calculating the structural stability of the community when the focal species i is removed. We then used a t-test to compare the contribution to stable coexistence of critical and non-critical species. More details about the calculation of structural stability can be found in the Supporting Information Section S4.

Finally, we wanted to understand how two species level control metrics are correlated with five metrics of keystoness based on centrality. The first control metric we use is a species control capacity ϕ. The second metric is the probability that a focal species influences the abundance of another species internally, regardless of whether a management intervention is required in that species or not. We call this the probability of being a superior node σ. Because superior nodes are those at the beginning of a matched link, σ could be seen as a "softer" version of control capacity. Conveniently, unlike the minimum driver node-set, superior species are the same for all control configurations and so in a network without reciprocal links the probability that a species is superior σ is either 1 or 0. Specifically, we compare a species control capacity ϕ and the probability that a species is used to internally control another species in the network being superior σ. As centrality metrics, we use a species' degree, betweenness, eigen centrality, page rank, and closeness centrality.

Testing assumptions

Just like the centrality metrics, the information obtained by applying structural controllability depends on the ability of the network to accurately represent the ecological community. We tested the sensitivity of our approach to two fundamental assumptions. First, we tested that visitation is an appropriate proxy to infer interspecific effects. To do that we compared the results obtained using visitation to two alternative metrics in a dataset that lacked invasive species (Ballantyne, Baldock, & Willmer, 2015). Specifically, we also applied the structural controllability approach to networks constructed using pollinator efficiency (which measures the pollen deposition of an interaction) and pollinator importance (which accounts for both pollen deposition and visitation and hence is regarded as a more accurate estimation of the pollination service received by plants; Ne'eman, Jürgens, Newstrom-Lloyd, Potts, & Dafni, 2009). More details in the Supporting Information Section S5. Second, because interspecific dependencies depend on the network topology and consequently on the accurate sampling of interactions, we tested the robustness of structural controllability to the uncertainty involved with the sampling of interactions. To do that we compared the results obtained when using the full network and when randomly removing interactions from the weakest links in the network. This effectively removed the rare interactions from the networks
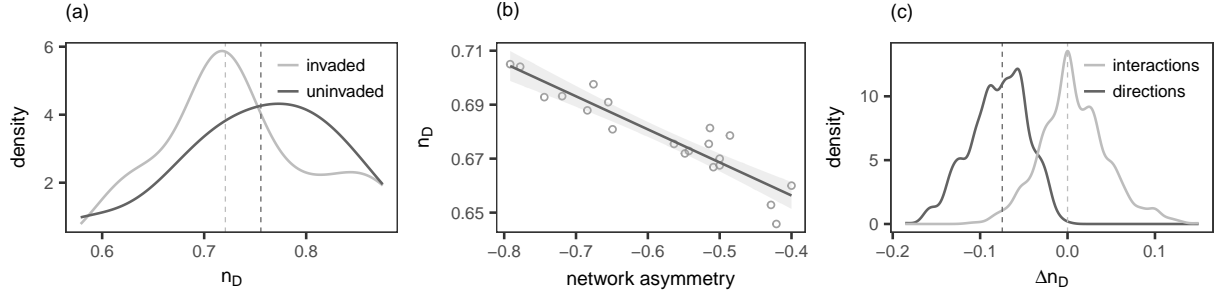
Figure 3: (a) Density plot of the relative size of the minimum driver node-set n_D in the invaded (light) and uninvaded (dark) empirical networks. (b) The relationship between the asymmetry plant/pollinator richness and n_D. The plot shows the values predicted by the most parsimonious model. (c) The density distribution of the difference between the relative size of the minimum driver node-set of random networks and that of empirical networks. We randomised either the species visitation patterns (light line) or randomised the direction of control between a species pair (dark line). The vertical dashed lines indicate the median values of each distribution.

277 (more details in the Supporting Information Section S6).

Results

278 The size of the minimum driver node-set relative to the number of species in each network n_D ranged

279 between $n_D = 0.58$ and $n_D = 0.88$ (median 0.74). We found that the relative size of the minimum driver

280 node-set of invaded communities was not significantly different from that of communities that have not

281 been invaded (Figure 3a). Contrastingly, there was an important negative relationship between n_D and

282 the network asymmetry (Figure 3b). Furthermore, there were also negative, albeit weaker, correlations

283 between n_D and connectance, nestedness and species richness (Table S3). The relative size of the minimum

284 driver-node set n_D of empirical networks did not differ to that of a null model that roughly preserved the

285 degree distribution and fully preserved the network connectance ($p = 0.66$; Figure 3c). However empirical

286 networks had a larger n_D than null models that preserved the interactions but shuffled the direction of

287 control of the empirical network ($p = 2.4 \times 10^{-7}$).

288 Species varied widely in their control capacity (Figure 4). Pollinators had, in average, larger control

289 capacities than plants but almost no pollinator was critical for network control (a species is critical for

290 control if it has control capacity of $\phi = 1$). Plants had a bimodal distribution with maxima in both

291 extremes of the distribution (Figure 4a). Remarkably, every invasive species was critical for network

292 control in each of their communities. The species level models indicate a positive relationship between

293 control capacity ϕ and a species' contribution to nestedness, visitation strength, and the asymmetry of

294 the dependence (Table 1; Figure 4; Table S4). Comparatively, species' degree was only weakly associated

295 with control capacity (Table S5). In fact, many species with a low degree, especially pollinators, attained

296 a large control capacity in their communities (Figure S10a).

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Table 1: Selection table of the generalised linear models of control capacity, ϕ. Only models with a weight larger or equal to 0.01 are shown.

				model terms								
int.	k	l	a	n	s	$k{:}l$	$l{:}a$	$l{:}n$	$l{:}s$	d.f.	ΔAICc	weight
-1.20		+	0.80	0.15	0.29		+	+		7	0.00	0.48
-1.19		+	0.76	0.13	0.35		+	+	+	8	1.52	0.22
-1.26	-1.24	+	1.44	0.39	1.07	+	+		+	9	4.09	0.06
-1.37	-0.66	+	1.03		1.06	+	+		+	8	4.39	0.05
-1.27	-1.15	+	1.37	0.33	1.07	+	+	+	+	10	4.92	0.04
-1.37	-0.10	+	0.90		0.43	+	+			7	6.36	0.02
-1.25	-0.28	+	1.24	0.40		+	+			7	6.47	0.02
-1.24	-0.62	+	1.29	0.38	0.40	+	+			8	6.50	0.02
-1.39	0.30	+	0.83			+	+			6	6.72	0.02
-1.28	-0.17	+	1.16	0.32		+	+	+		8	7.03	0.01
-1.26	-0.53	+	1.23	0.32	0.39	+	+	+		9	7.42	0.01
-1.02		+	0.69	0.30	0.31		+			6	7.48	0.01

Terms: intercept (int), degree (k), trophic level (l), asymmetry (a), contribution to nestedness (n), visitation strength (s).
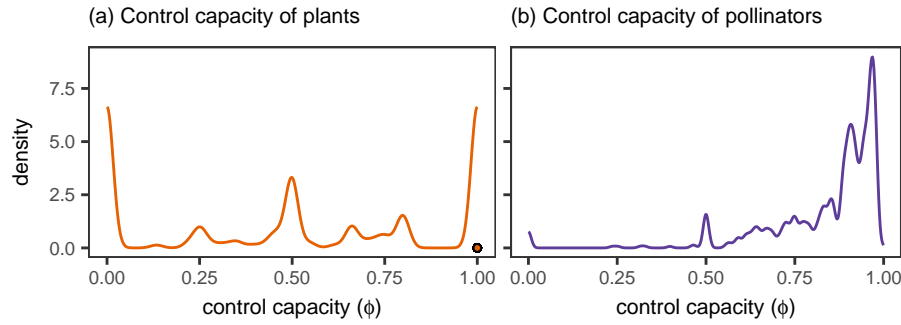

Figure 4: Density plot of the control capacity ϕ of (a) plants and (b) pollinators. The control capacity of all invasive species is $\phi = 1$ and is depicted with solid circles.
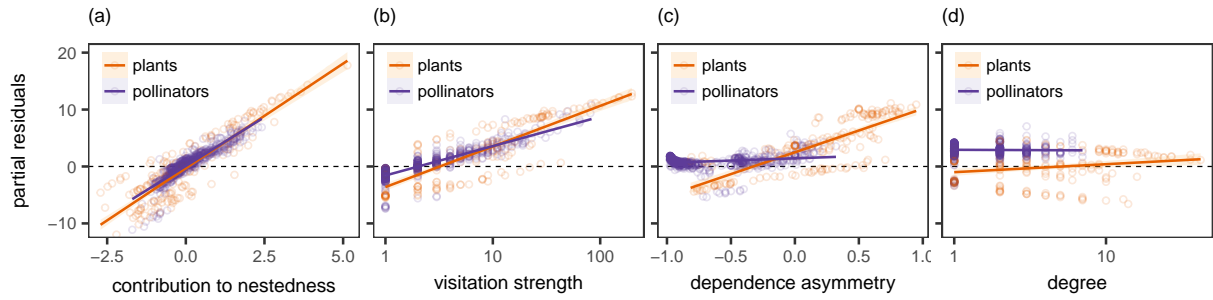

Figure 5: Model averaged partial residual plots for the relationship between control capacity and (a) contribution to nestedness, (b) visitation strength, (c) asymmetry of dependences, and (d) degree.

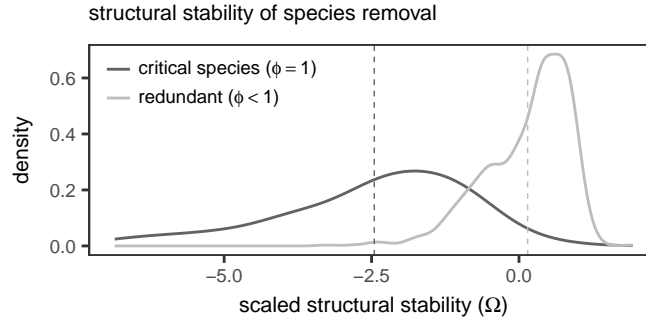structural stability of species removal

Figure 6: Density plot of the structural stability of the communities after a focal species is removed. The structural stability after critical species have been removed (darker line) is considerable smaller than the average. To allow comparison across communities, the structural stability values were scaled within each network to have a mean of 0 and a standard deviation of one.

We also found that critical species have a large impact on species coexistence. Indeed, the structural stability of the network was considerably reduced when these species were removed from their communities ($p = 3.3 \times 10^{-16}$; Figure 6; Supporting Information S4).

The control capacity of a species ϕ was only weakly correlated with commonly used centrality metrics. The Spearman correlation ranged between -0.14 (with betweeness-centrality) and 0.42 (with eigen-centrality). On the other hand, the probability of being a superior species σ was slightly more similar to established centrality metrics. The Spearman correlation coefficient ranged between 0.07 (with eigen-centrality) and 0.75 (with degree; Figure S11). Despite the higher correlation with species' degree, with the exception of specialists that had only one interaction, we observed many species with a low degree and a high probability of being superior nodes (Figure S10b).

We found that using visitation as a proxy for the strength of species interactions leads to similar results than those obtained using pollinator importance (regarded as an accurate measure of the pollination service to plants; Supporting Information Section S5; Ne'eman et al., 2009). Importantly, we also found that structural stability is robust to incomplete sampling of interactions. We found a very strong agreement between results obtained using the complete empirical networks and those obtained by randomly removing interactions (Supporting Information Section S6). Despite removing rare interactions and species, the relative size of the minimum driver node-set, the superior species, and the relative rankings of control capacity were generally maintained. Remarkably critical species in the full network were also critical in the vast majority of rarefied networks.

Discussion

Our main goal was to understand the role that species play at both modifying the abundance of the species they interact with and the state of the community as a whole. To achieve that goal we applied

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Table 2: Glossary

network control
A network is said to be controllable if it is possible to steer it from an initial to an arbitrary final state within finite time.

controllability
The intrinsic difficulty of controlling an ecological community. It is measured by the relative size of the minimum driver node-set, n_D. It also indicates the extent to which network structure can be harnessed for network control.

minimum driver node-set
One of the often many smallest sets of species whose abundances need to be directly managed in order to achieve full control of the community. The minimum driver node-sets can be obtained by finding all maximum matchings in a network.

maximum matching
A matching is a set of links that do not share a common start or end nodes; the largest possible matching is called a maximum matching.

control configuration
One of the species combinations with which is possible to achieve network control. Optimal control configurations are given by the minimum driver node-sets.

control capacity
The relative frequency ϕ which with a species is part of the optimal control configurations of a network.

critical species
A species with the maximum control capacity $\phi = 1$

superior node
A species is a superior node if it that can internally affect the abundance of other species in the network. Superior nodes make up the chains that propagate the control signals through the network.

³¹⁸ *structural controllability*, a field at the intersection between control and complex theory that allow us

³¹⁹ to obtain two key pieces of information: the *controllability* of a network and a species *control capacity*

³²⁰ (Table 2).

³²¹ The median size of the relative minimum driver node-set of in our dataset was $n_D = 0.74$. This value is

³²² high when compared to other complex systems in which controllability has been investigated.

³²³ For instance, only gene regulation networks appear to achieve similar levels of controllability while most

³²⁴ social, power transmission, internet, neuronal, and even metabolic networks seem to be easier to control

³²⁵ $(0.1 < n_D < 0.35)$ (Liu et al., 2011). These results indicate that fully controlling ecological networks might

³²⁶ currently be out of reach for all but the smallest communities (A. E. Motter, 2015). Nevertheless, structural

³²⁷ controllability might be helpful at identifying communities in which changes in the ecological state are

³²⁸ more likely to occur and provides solid theoretical explanation to the many difficulties encountered in the

³²⁹ management and restoration of natural communities.

³³⁰ When controlling for network structure, we found no difference between the controllability of invaded and

³³¹ uninvaded networks. Our results suggest that the differences between the controllability networks are

³³² instead likely to arise from differences in their structure. Specifically, we found that network controllability

is almost completely constrained by the patterns of species richness at each trophic guild and their degree distributions (N. Blüthgen et al., 2007; C. J. Melián & Bascompte, 2002). These two factors are particularly relevant because they govern the asymmetric nature of mutual dependences-which constitute the foundations of structure and stability in mutualistic networks (Astegiano, Massol, Vidal, Cheptou, & Guimarães, 2015; J. Bascompte et al., 2006; J. Memmott, Waser, & Price, 2004).

Accordingly, our results suggest that structural controllability is closely related to the persistence of an ecological community. First, we found a comparatively small but tantalising negative relationship between the controllability of a network and the nestedness of its interactions. Previous studies indicate that nestedness promotes species coexistence and confers robustness to despeciation (Bastolla et al., 2009; J. Memmott et al., 2004) at the expense of the dynamic stability of the mutualistic community (S. Saavedra et al., 2016). These observations are in agreement with our results, as we would expect the dynamic stability of a community to be correlated to the difficulty to control it. Second, species' control capacity was strongly correlated to their contribution to nestedness and critical species had the largest impact to the stable coexistence of species in their communities. Therefore, species that play a key role at determining the state of the community might also be more key to "maintain the organization and diversity of their ecological communities", one of the hallmarks of keystone species (Mills & Doak, 1993).

When controlling for a species' strength (which is indirectly a proxy of its abundance) and the net balance of its dependencies, we found that control capacity could not be easily predicted by species' degree or other metrics of centrality. For instance, some species with a low degree achieved the maximum control capacity and were critical for control in their communities. At first glance, our findings challenge numerous studies that highlight the role that central species play in the dynamics of their communities and their utility at predicting species extinctions (Jordan, 2009). However, further inspection shows that our results do not contradict these findings. On the contrary, most species with a large degree also have a large control capacity and all of them were classified as superior nodes which corroborates the utility of classic centrality metrics. What our results do, is to take previous findings one step further and suggest that centrality might paint only a limited picture of the relevance of species.

Other conceptual differences between structural controllability and centrality metrics might provide further insight into the conservation of ecological networks. First, structural controllability emphasizes that the effect a species has on the abundance of other species is not independent of the effects of other other species in their community. Second, it demonstrates that to ensure the persistence of a community it is often necessary to consider the abundances of more than a single species, even when full control is unfeasible or undesired (for example 90% of our communities contained more than one critical species). Third, structural controllability explicitly acknowledges the existence of multiple management strategies and some will be better than others depending on the context. Approaches to prioritise species for

conservation and reintroduction based on traits or centrality are still useful and are likely to overlap with a species' control capacity (Devoto, Bailey, Craze, & Memmott, 2012; Pires, Marquitti, & Guimarães, 2017). Altogether, our results also provide support to the idea that management decisions should not be based on a single technique, but indicates that focusing on ecosystem processes and interactions may be more effective than traditional ranking based approaches (Harvey, Gounand, Ward, & Altermatt, 2017).

The choice of the invaded/uninvaded networks was based on our desire to contrast the extensive empirical evidence of the role of invasive plants with our theoretical results. We found that without exception, invasive plants were critical for network control and as such our results were in line with our expectations. Invasive plants have been previously found to exacerbate the asymmetries in their communities (Aizen, Morales, & Morales, 2008; bartomeus_contrasting_2008-1; Henriksson, Wardle, Trygg, Diehl, & Englund, 2016) and to be central in their communities (Palacio, Valderrama-Ardila, & Kattan, 2016; Vila et al., 2009). We found that invasive plants are, however, unlikely to be inherently different from their native counterparts (Emer, Memmott, Vaughan, Montoya, & Tylianakis, 2016; Stouffer, Cirtwill, & Bascompte, 2014). Just like any other mutualist in our dataset, invasive plants tended to attain a high control capacity proportional to the degree to which they contribute to network persistence, are abundant, and depend little on other species. Furthermore, our observation that changes in the abundance of invasive plants (and presumably all critical species) are crucial to modify the state of the community agrees with recent evidence showing that ecosystem restoration focused on the eradication of invasive plants can have transformative desirable effects in plant-pollinator communities (Kaiser-Bunbury et al., 2017). However, our results also suggest that removals must be exercised with caution. Not only it is hard to predict the direction in which the system will change, but we also show that critical species can underpin the coexistence of species and therefore some communities may be acutely vulnerable to their eradication (Albrecht, Padron, Bartomeus, & Traveset, 2014; Traveset et al., 2013).

Structural stability assumes that the networks can be approximated using linear functional responses. The ramifications of this assumption imply that while structural controllability is useful to identify species that are relevant for network control, it cannot be used to design the precise interventions that should be applied to these species in order to achieve a desired state. While in an ideal scenario we would completely incorporate the species dynamics into the controllability analysis (Cornelius, Kath, & Motter, 2013), the reality is that such information is rarely available in most ecological scenarios. In contrast, structural controllability only requires a quantitative approximation of the network's interactions to gain valuable insight from the community. Furthermore, unlike centrality metrics, the assumptions of structural controllability are explicit and the estimation of a species importance arises from a mechanistic understanding of the population dynamics between species. By accounting for network dynamics (even if in a simple way) it incorporates more ecological realism even in the extreme scenario where the state

of a community depends almost exclusively on nodal dynamics rather than on the topology of their interactions.

Here we show that structural controllability can be applied in an ecological setting to gain insight into the stability of a community and the role that species play at modifying the abundance of other species and ultimately the state of the community. These characteristics make structural stability an ideal framework to evaluate the effects of invasions and other types of perturbations. Importantly, structural controllability can be used to identify critical species in the community. Critical species promote biodiversity and underpin the stable coexistence of species in their community. Collectively critical species dominate the state of their community and therefore are likely to be highly relevant for ecosystem management and conservation. Centrality metrics which have often been used as a proxy for keystoneness, although useful, fail to identify some of these species which highlights their limitations when we embrace that ecological communities are dynamical systems. Paine (1969) showed nearly 50 years ago that one single species can dominate the state of its community. Structural controllability suggests that this situation might be the exception rather than the rule. We see our study as a starting point to study the controllability of ecological and socio-ecological systems where many exciting questions lie ahead.

Awknoledgements

Author contributions

All submissions with more than one author must include an Authors' contributions statement. All persons listed as authors on a paper are expected to meet ALL of the following criteria for authorship:

- substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data, or drafting the article or revising it critically for important intellectual content;
- final approval of the version to be published;
- agreement to be accountable for the aspects of the work that they conducted and ensuring that questions related to the accuracy or integrity of any part of their work are appropriately investigated and resolved.

Acquisition of funding, provision of facilities, or supervising the research group of authors without additional contribution are not usually sufficient justifications for authorship. The statement should include an explanation of the contribution of each author. We suggest the following format for the Authors' contributions statement:

AB and CD conceived the ideas and designed methodology; CD and EF collected the data; EF and GH analysed the data; AB and CD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

To enable readers to locate archived data from papers, we require that authors list the database and the respective accession numbers or DOIs for all data from the manuscript that has been made publicly available. Please see our editorial policies page for further information

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