Structural controlability of pollination networks

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Alternative titles:

Structural controlability of ecological networks

Network manageability in the context of species invasion

Biotic invasions reduce manageability of ecological networks

Identifying the "driver species" of an ecosystem

Introduction

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

Seminal work on control theory has established a strong link between the structure of complex networks and its controlability and that in principle it is possible to alter any ecological community's composition, by modifying the abundances of just some key species (Liu, Slotine, and Barabási 2011; Cornelius, Kath, and Motter 2013). Based on this work and using a small number of binary food-webs (only presence or absence of interactions), it has been suggested that the degree distribution of ecological networks makes them inherently difficult to control (Liu, Slotine, and Barabási 2011; Ruths and Ruths 2014). This theoretical result is in agreement with many cases in which the management of ecological communities is more challenging than aticipated. In contrast with other types of complex systems like neural, intra-organizational, or trust neworks, ecological networks do not have a hierarchical or distributed structuretend 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 add ref

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 variablity of their structure and interaction strengths—which can vary by several orders of mangitude. `add ref`

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, Eskildsen, 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 abbundances of one species may ripple trough 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. `is this too harsh?`

Here, we expand previous theory of the control of complex systems and use a set of paired invaded and uninvaded plant-pollinator communities to investigate the link between network structure and our ability to manage them. Plant-pollinator networks provide an ideal framework to answer these questions. On one hand, community networks that quantify relative levels of interaction are readily available. On the other, the bipartite nature of pollination networks makes it is possible to simplify assumptions of how these interactions translate into interspecific effects. Our theoretical extension of network control, allow us to ask the question of whether biotic invasions as drivers of change in network structure increases or decreases the manageability of communities as well as the relative importance of species at driving the population
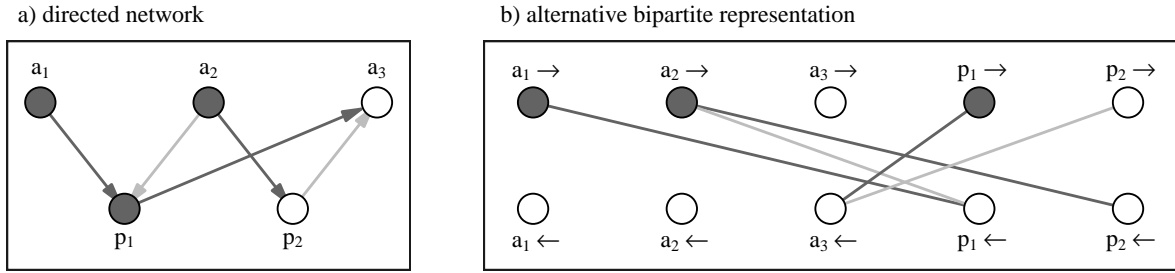
Figure 1: One of the possible maximum matchings of a network (dark grey links) defines a set matched (p_1, p_2, and a_3) and unmatched nodes (a_1 and a_2). The minimum number of species neccessary to control this network equates to the number of unmatched nodes $n_d = 2$. Superior nodes (dark grey circles) drive the dynamics of other species and are therefore important for the controlability of the network because they either require external input or because the are part of the chain that transmit the external imputs to other species.

dynamics of other species in the community. .

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Theory of community manageability

Maximum matching

The number of nodes necessary to fully control a complex network can be calculated by counting the number of unmatched nodes in the network's maximum matching (Liu, Slotine, and Barabási 2011). In a directed network a matching is a subset of links in which no two links share a common starting node or a common ending node; a node is matched if it is the ending node of one of the links in the matching (Figure 1a). A matching is then maximum if *(i)* the number of matched liks—also 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 (West 2001). To find the maximum matching we used an alternative bipartite representation of the network in which the two levels indicate the outgoing and incoming links to each node (Figure 1b). Finding a matching in this alternative representation is equivalent to finding the set of links such that each node on the top level is matched to at most one node on the bottom level, and vice versa (West 2001; Csardi and Nepusz 2006).

Given a maximum matching, the link to network controllability has a relatively straightforward and intuitive basis. In control theory, a network is fully controlable when each node has a "superior", this is, an input that drives its dynamics. Matched nodes can thus be controled by the node pointing to it—its superior. Unmatched nodes on the other hand, have no superior in the network and must be directly controlled by external inputs (Liu, Slotine, and Barabási 2011). In an ecological context, this is what we refer to as management interventions.

Systems that require a large number of external inputs are more difficult or costly to control. The *manageability* of a community m is therefore determined by the proportion n_d of species on which we would
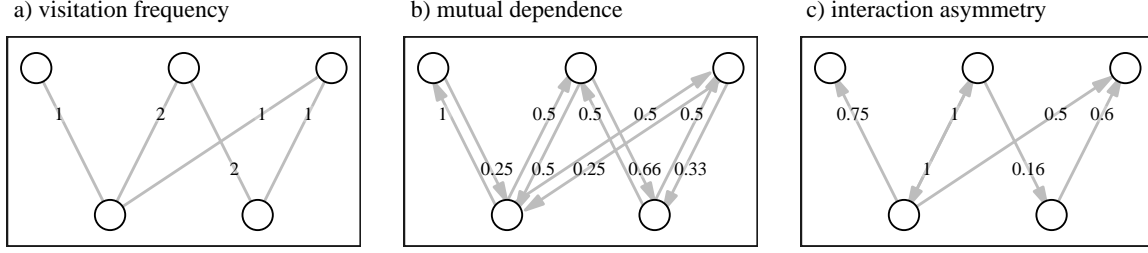
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Figure 2: Mutualistic networks are usually described quantitatively by the relative number of visits between each plant and animal species (a). The mutual dependencies between interacting species (b) depend directly on the relative visitation frequency. The dependency of plant i on pollinator j, d_{ij}, is the proportion of the visits coming from pollinator j compared to all pollinator visits to plant i. Likewise, the dependency of pollinator j on plant i, d_{ji}, is the ratio of the visits by pollinator j to plant i and all visits of pollinator j. Nevertheless, mutual dependencies in pollination networks tend to be highly assymetric. The relative differences of dependencies (c) then is a good indicator

need to apply management interventions in order to gain full control of the abundances of all species in the ecological community,

$$m = 1 - \frac{n_d}{s},$$

where s is the total number of species in the community.

Weighting links

Recall that our maximum matching algorithm requires a directed network in which a link between species i and j pointing to species j indicates that the abundance of j can be affected by the abundance of i. In ecological networks, establishing a directionality for the links between species is relatively straightforward when they represent resources or energy flow, however, interspecific effects—particularly in pollination networks— are not strictly directed. Nevertheless, the extent to which a pair of interacting species affect each other can be quantified by the magnitude of the mutual dependence (Bascompte, Jordano, and Olesen 2006). As the dependencies are bidirectional, this assumption renders a bipartite network in which interacting pairs are connected by two directed links (Figure 2b).

Nevertheless, mutual dependencies have been shown to be highly assymetric in natural communities (Bascompte, Jordano, and Olesen 2006). In other words, if a plant species is largely dependent on a pollinator species, then the pollinator tends to depend only very weakly on the plant. This suggest that it may be possible to relax our initial assumption and simplify the network such that interacting species are connected by one directed link when mutual dependencies are highly assymetric (Figure 2c). The extent to which a species i affects species j relative to the extent to which species j affects species i can then be summarised by the interaction asymmetry.

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

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Relative importance

insert ecological motivation?

The manageability of a community m provides an indication of the magnitude of n_d but not the identity of the species that compose this set. Moreover, maximum matchings are often not unique in for a given network and different sets of species of size n_d could be used to control the network (Liu, Slotine, and Barabási 2011). Species vary in terms of the frequency with which they are classified as superior nodes (Figure 1), and this frequency provides an indication of their relative importance in driving the state of the community.

We therefore call *driver species* those that are identified as being a superior node in all possible match- check ings, and consequently likely to have a disproportionate effect on the abbundances of other species in the community. Unlike unweighted networks, where a maximum matching is defined by its matching size (the number of matching links), a maximum matching in a weighted network is one whose links have the largest possible total weight among all possible matchings. This means that in weighted networks there is a number of matchings that have maximal size, but are not maximum matchings because their total weight is not maximal.

Consequently, we identified the driver species in each of the networks by computing all possible matchings in the network that have the same maximal size while allowing for some tolerance regarding the weight. We relax the matching weight requirement because empirical intreaction strengths, from which we calculate dependencies, are stochastic to some extent and depend on the sampling method and intensity. To compute all the matchings with maximal size, we first generated the network's line graph—an alternative representation in which nodes are the interactions of the original network and links represent common ending points. We then calculated the complement of the line graph—a graph in which nodes are adjacent if and only if they are not adjacent in the line graph. All possible maximum matchings can be found by enumerating all cliques of size $1 - n_d$ in this complement graph (West 2001; Csardi and Nepusz 2006).

Methods

In the last section we outlined the theoretical and computational underpinings of our approach. Now we illustrate its empirical application using ten pairs of plant-pollinator communities for which we calculated their manageability and the relative importance of species. Each network pair was composed by a community invaded by a plant and a community effectively free of the invasive species (Table S1). The networks were constructed from previously published visitation data collected from pollination communities in Bristol, UK (Lopezaraiza-Mikel et al. 2007) and in Cap de Creus National Park, Spain (Bartomeus, Vilà, and Santamaría 2008). In the four British uninvaded communities, the non-invaded plots were obtained by

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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 these networks was determined using visitation frequency which has been shown to be an appropriate surrogate for inter-specific effects in pollination networks (Vázquez, Morris, and Jordano 2005; Bascompte, Jordano, and Olesen 2006). To examine the importance of this decision, we also evaluated the effect of using pollinator efficiency or importance as alternative measures of species interactions (Ne'Eman et al. 2010; Ballantyne, Baldock, and Willmer 2015), and we found consistent results for all of these options(see Supplementary Information).

Community manageability

We started by quantifying the manageability of the analysed pollination communities. To do that, we calculated the maximum matching of the corresponding pollination network, and estimated the minimum number of species that need directed intervecntions to fully control the species abbundances in the community. If a network had more than one component (two species are in different components if there exist no path between them) we analysed the largest one. Although understanding the distribution of manageability across ecological networks is an useful result in itself, we wanted to test wheter perturbations, like invasion status, have an impact on manageability values. As, naively one might expect to see a negative relationship between diversity and manageability (Menge 1995), we used a set of generalised linear models (with binomial error structure) to investigate the effect of invasion status while controling for *(i)* the total number of species, *(ii)* plant richness, *(iii)* polinators richness, *(iv)* the ratio of plants to pollinators richness, and *(v)* the study site. Competing models were assessed by comparing the Akaike Information Criterion corrected for small sample sizes (AICc).

Subsequently we explored the extent to which structural factors in the empirical networks influence their manageability. Previous studies found a direct link between a network's degree distribution and the number of nodes necessary to fully control it (Liu, Slotine, and Barabási 2011), but this relationship has not been explored in weighted ecological networks. We therefore compared the manageability of the empirical networks to networks generated by three null models. One set of random visitation networks was generated by maintaining each species' degree (its number of interactions) while varying the number of visits per species. A second set of random networks mantained the species' strength (its total sum of visits) while varying their degrees. Randomisations were generated using vegan 2.3-3 (Oksansen et al. 2016). Finally a three set of fully random networks maintained only the connectivity of the empirical network, but both degree and weight were allowed to vary. We then calculated the mutual dependences and interaction asymmetries of the random networks and calculated their manageability using the maximum matching algorithm. Finally we calculated the p-value of the manageability of each empirical network and the corresponding manageability of 999 randomisations.

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

Relative importance of species

Our third question is related to how different species differ on their importance for the population dynamics of the community. To quantify this importance we computed all possible matchings that have the same size as the maximum matchings and in each network. We then calculated the frequency to which each species is deemed to be a superior node in matchings with a weight equal or larger to 0.5 times the weight of the maximum matchings. We choose this threshold as it provided a high agreement between the relative importance of species calculated by weighting interactions with the mutial dependencies or the depndence asymmetry as well as between the network is quantified by visitation or pollination efficiency. Nevertheless, the choice of the threshold only had a negligible impact on the results (Supplementary information).

The number of maximal matchings increases exponentially with the number of links and nodes in a network. When we use mutual dependecies, the large number of links in the most diverse communities renders the computation unfeasible. Taking this limitation into account we compared the relative network manageability obtained when using assimetries or when using mutual dependencies for eleven networks—for which the number of matchings was smaller than 4×10^{10}. Results from a paired Spearman correlation test, the weighted correlation coefficient r_{w2}—which gives more weight to higer ranks (Pinto Da Costa, Roque, and Soares 2015), and the Jaccard similarity of the driver species in both approaches, suggested a high similarity in relative ranks. Therefore, we used the results from the assymetries, rather than mutiual dependences, to further investigate the factors that determine species' relative importance.

We then asked the question of whether some species-level structural properties can predict the relative importance of species. Here, we used a Generalised Linear Mixed-Effects model to evaluate the effect on the species' relative importance of a suite of structural measures. We included measures of centrality (degree and eigen-centrality) which have been found to be strong predictors of importance in a coextintion context; [add ref] measures related to network robustness (contribution to nestedness) as nestedness has been proposed as one of the key properties that promote stability in mutualistic networks (Saavedra et al. 2011); and measures of strength of association and depedency (visitation and dependency strength) as their skewed distribution is characteristic of plant-pollinator networks and determine the extent of interspecific effects. All metrics were calculated using bipartite 2.06 (Dormann, Gruber, and Fründ 2008). To allow for variation among different ecological communities, this factor was included as a random effect (Bates et al. 2015). Candidate
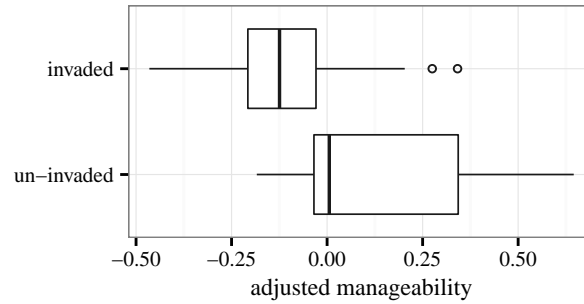
Figure 3: Invaded communities have lower levels of manageability than uninvaded communities even when controling for the ratio of plant to pollinator richness. Adjusted manageability corrsponds to the partial working residuals of the invasion status.

models were compared using AIC and the relative importance of the explanatory variables was evaluated using the sum of Akaike weights over candidate models that accounted for 95% of the evidence (Burnham and Anderson 2003; Bates et al. 2014; Bartoń 2016).

Invasive species have been shown to have disproportionate effects on the communities they invade. So we examined the extent to which invasive species tend to be driver species—species whith the maximum importance. As our invasive species were plants, we compared the relative importance of invasive species to those of other plants in the community and to which degree they differ when accounting for the structural factors that determine their importance.

needs to be developed once the results section is rewritten

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

Results

Community manageability

The studied networks had levels of manageability between 0.12 and 0.58 (mean 0.37) when we considered bidirectional links weighted by the mutual dependences. This was in strong agreement to the results obtained using the dependence asymmetry in which manageability ranged between 0.08 and 0.45 (Spearman rank correlation 0.93, $p = 1.7 \times 10^{-9}$). In addition we found that even when controling for diversity, invaded communities had were more difficult to manage than uninvaded ones. Out of the explored factors—total number of species, plant richness, pollinator richness and the ratio of plant to pollinator richness—only the ratio of plants to pollinator was retained in the final model (as determined by the AICc; Figure 3, Table S3).

The manageability of empirical networks was, in general, not significantly different to the manageability of network randomisations that maintain the degree or the strength of individual species (Figure 4). However when comparing the empirical network to less constrained randomisations that maintained the original connectance but in which species had different degrees and strengths, we found that empirical networks tend to have smaller values of manageability. This pattern is even more marked when we maintained the network
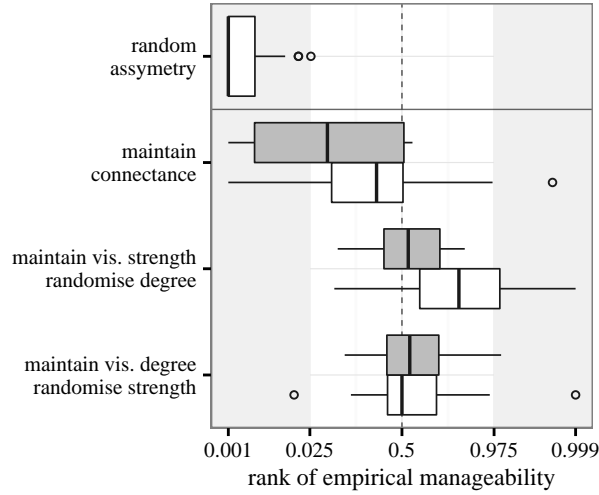
Figure 4: The manageability of empirical networks was compared to network randomisations using a normalised rank. The shaded areas in light grey (< 0.025 and > 0.975) suggest a significant difference between the empirical network and its randomisations. The empirical manageability is much smaller than those of randomisations in which the direction of assymetries has been randomised. In contrast the manageability of network in which the visitation strength or degree was mantained was not different to the manageability of the empirical networks. Dark grey and white boxplots represent manageabilities obtained using mutual dependencies and asymmetries respectively.

structure but randomised only the direction of the asymmetries (Figure 4).

Relative importance of species

We found a strong agreement between relative species' importance in the 11 networks for which we were able to calulate it using both mutual dependencies and asymmetries (Spearman's rank correlation ranged between $\rho = [0.6, 0.78]$, median $\tilde{\rho} = 0.69$). Indeed, when using the weighted rank correlation coefficient r_{w2}, we found that the agreement was stronger for highly ranked species than for lowly ranked species ($\tilde{r_{w2}} = 0.72$ versus $\tilde{r_{w2}} = 0.59$). Moreover both approaches identified a highly similar set of driver species (Jaccard similarity $J = [0.5, 1]$, $\tilde{J} = 0.67$). Therefore we employed the relative rankings obtained using asymmetries in the following analyses.

Although plants showed significantly higher levels of importance than pollinators (Mann-Withney-Wilcoxon test, $p < 0.001$), this difference can be largely explained by the strength of dependency of the species (the sum of the dependencies for a given species). Indeed, when averaging over the set of GLMMs that accounted at least 95% of the evidencee based on AICc, we found that the strength of dependency is the single most important factor determining the relative importance of species for network control (Table 1, Figure 5). In contrast, the number of visits a species makes (or receives) and its contribution to nestedness have only a marginal effect on its relative importance.

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In addition, in the ten communities that were invaded, invasive species were invariably classified as a driver species. In general, the relative importance of invasive species was significantly larger than those of the other plants in the studied communities(Mann-Whitney U Test, $p = 0.02$). However this difference can

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

Table 1: The strength of dependency, contribution to nestedness and visitation strength had a significative effect on all the models that accounted for 95% of the evidence based on AICc. Coeficient estimates were avaraged following Buckland, Burnham, and Augustin (1997); confidence intervals were calculated following Lukacs, Burnham, and Anderson (2010).
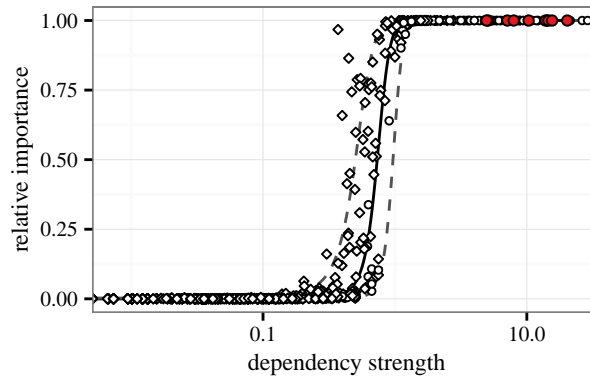
Figure 5: Dependency strength is the single most important factor explaining the importance of species for network control. Visitation levels and contribution to nestedness had a significant albeit small effect on the importance (dashed lines correspond to ±one standard deviation on these factors). Invasive species (red) were invariably classified as driver species (those having the maximum importance for network control.

be fully explained by the explanatory variables in our model as all the residuals for the invasive species were virtually zero.

Discussion

We found that

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

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

Acknoledgements

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