An empirical attack tolerance test impacts network structure and triggers asymmetrical reorganization

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May 5, 2020

Abstract

Ecological network theory hypothesizes a link between structure and stability, but this has mainly been investigated in-silico. In an experimental manipulation, we sequentially removed four generalist plants from real plant-pollinator networks and explored the effects on, and drivers of, species and interaction extinctions, network structure and interaction rewiring. Cumulative species and interaction extinctions increased linearly with removing plants, and both species and interactions disappeared faster than expected by co-extinction models, which even predicted several false cases. Networks were not stable and symptoms of fragility emerged with removing plants: nestedness decreased, modularity increased, and opportunistic random interactions and structural unpredictability emerged. Conversely, interactions reorganization ("rewiring") was high, asymmetries between network levels emerged as plants increased their centrality and no change was found in stochastic robustness index. Our study shows that experimental manipulations of real networks indicate how species and interaction occurrences are altered when key resources are removed from the system.

Introduction

The patterns of ecological interactions that emerge after disturbances provide information on the ability of systems to keep functioning or to collapse (Memmott *et al.* 2004; Kaiser-Bunbury *et al.* 2010; Santamaría *et al.* 2016). However, it is hard to predict the consequences of extinctions and co-extinctions on the establishment of interactions and on species survival. Also, the buffering capacity resulting from the re-organization of interactions by using new resources is not well understood (Brodie *et al.* 2014; Biella*et al.* 2019b; Vizentin-Bugoni *et al.* 2019). Yet, insights into the network responses to species loss will lead to more efficient conservation decisions based on the ecological role of species (Pigot*et al.* 2016; Biella *et al.* 2017; Brodie *et al.*2018).

For understanding the consequences of species loss on ecosystem functioning and for planning conservation and restoration measures, the root mechanisms underlying network structure and interaction dynamics have to be described first. One such mechanism is the foragers' ability to exploit novel resources when the former ones are depleted or disappear after a disturbance event (Valdovinos *et al.* 2013; CaraDonna *et al.* 2017), so called interaction "rewiring". Yet, describing this rewiring seems particularly challenging, especially when interactions are complex and involve multitudes of species with heterogeneous traits, local population sizes, and life history characteristics (Vizentin-Bugoni *et al.* 2014; Timoteo *et al.* 2018). So far, ecologists have used a range of methods to explore this topic. For example, responses to simulated anthropogenic disturbance *in silico* have provided some general insights into the resilience of species networks to disturbances and

extinctions (Pocock *et al.* 2012; Evans *et al.* 2013; Fortuna *et al.* 2013). In the field, species and interaction turnover triggered by ecological or habitat alteration gradients has been used to investigate the mechanisms of the assembly and disassembly of interaction networks (Sabatino *et al.* 2010; Carstensen *et al.* 2014; Nielsen & Totland 2014). However, manipulative experiments have the greatest potential for understanding causal relationships and identifying the processes leading to rewiring and species co-extinction, but the few studies performed so far involve small-scale or light manipulations and often show contradictory results (Ferrero *et al.* 2013; Goldstein & Zych 2016; Kaiser-Bunbury *et al.* 2017; Stavert *et al.*2019). So far, the heterogeneity of the approaches used in previous studies, the difficulty of an ecologically-meaningful interpretation of network indices, and the challenges of field-testing the reliability of computer-based simulations have prevented clear conclusions to be drawn. Thus, deeper field manipulations are needed, from which mechanisms governing network structure could be inferred and used as a tool for ecological conservation.

In this study, we performed an attack tolerance test on real plant-pollinator networks. An attack tolerance test is usually aimed at verifying whether the functionality of a system is maintained after knocking down several of its important components (Burgos *et al.*2007). For plant-pollinator networks, this topic was investigated by relating the amount of co-extinctions to robustness and redundancy within networks (Dunne *et al.* 2002). However, this has been addressed only theoretically with numerical simulations of sequential species extinctions in a trophic level and afterwards calculating the fraction of species that lost all interactions (Memmott *et al.*2004; Kaiser-Bunbury *et al.* 2010; Fortuna *et al.* 2013). In this study we set up a field experiment in which generalist plant species were sequentially removed in order to investigate the consequent effect on plant-pollinator networks and rewiring, and on extinctions of species and interactions. This experiment is the first one involving such deep alterations of a plant-pollinator network by sequentially removing as many as four of the most generalist plants.

It can be expected that after removing key floral resources, several pollinators will either disappear from the network or they will start utilizing alternative resources at higher rate. In the latter case, if high interaction shifts (i.e., rewiring) take place as a result of adaptive foraging (Valdovinos *et al.* 2013), the network modularity (i.e., compartmentalization of a network as a result of selectivity for food sources) will decrease because foragers will use a progressively broader range of the remaining resources (Thebault & Fontaine 2010). In contrast, as core generalists usually occupy a central position in a network and keep it cohesive (Jordano *et al.* 2006), and a network could fragment into disconnected units when such core elements are removed (Reis *et al.* 2014). This would result in a higher modularity and specialization, as interactions will be segregated uniquely within isolated compartments.

To test these hypotheses, during the sequential removal experiment we investigated (a) if the extinction rate of species and interactions is similar to what is expected from simulations *in-silico* ; (b) alterations in the structure of plant-pollinator networks and the rate of interaction rewiring; and (c) what ecological factors (species abundance, morphology, amount of sugar in the nectar) can explain these changes.

Material and methods

The study included three treatment and one control sites, located at a mean distance of 2.01+-0.95 km from each other, near Český Krumlov, in the Czech Republic (treatments: 48°49'26.8"N-14°16'26.2"E; 48°49'51.63"N-14°17'34.12"E; 48°49'35.07"N-14°18'8.2"E; control: 48°49'26.8"N-14°16'26.2"E). Each site was a small grassland with a barrier of trees (see details in Biella *et al.* 2019a). The experiment consisted of sequentially removing all inflorescences of the most generalist plant species from the entire surface of the treatment sites, one species at a time until four species were removed. We sampled flower-visiting insects in six 10m x 1m transects per site during two days for each experimental phase (before and after each species was removed), and synchronously in the control site. After each "before" phase, flower-visitors were counted and this was used as a proxy of generalization to determine which plant species to be removed; as detailed in Biella *et al.* (2019a), this proxy was reliable and in fact we later verified that these plants were visited by the most diverse set of pollinators, similarly to Goldstein & Zych (2016). We identified all insects to species where possible, otherwise morpho-species were used when necessary (after pre-sorting into families and genera). In addition, we counted the number of flowers or inflorescences of all plant species within transects over the

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sampling period.

Species co-extinctions

We compared the rate of pollinator and of interaction extinctions from the field after the removal of each generalist plant to what was expected from two co-extinction models, the Topological (TCM, Memmott *et al.* 2004) and the Stochastic co-extinction models (SCM, Vieira & Almeida-Neto 2015). TCM is based on the topology of a qualitative binary network and secondary extinctions (i.e. pollinators) are considered as when a species has no surviving partners after a primary extinction has occurred (i.e. plants). The SCM uses quantitative data, as it calculates an extinction probability based on the interaction strength between species and the dependency on the interaction (R), and allows cascading extinction chains (Vieira & Almeida-Neto 2015). Separately for each plant removal stage of the treatment sites, these co-extinction models were triggered by removing the same generalist plant species as the field manipulations, and the number of extinctions were counted. In the SCMs, we ran 10^3 SCM simulations, and, following Dalsgaard *et al.* (2018), we assigned random R values to plants and pollinators, and later grouped each of them in either "low" (R =[0-0.33]), "low-medium" (R =[0-0.66]), "medium" (R =[0.33-0.66]), "medium-high" (R =[0.33-1]) or "high" (R =[0.66-1]).

We counted as extinctions the number of pollinators or the amount of interactions recorded before a plant removal that did not occur after a plant removal, for both the observed networks and the models. To avoid overestimations, in the observed networks we considered (i) as extinct species those pollinators that had interacted with the plant targeted of removal that were not recorded after the removal, and (ii) the interactions of those pollinators that occurred in both before and after removal phases and of those ones that had interacted with the plant removed. In addition, all singletons (i.e. species with interaction abundance of 1) were removed from the observed networks and also from the simulations, to avoid overestimations due to species with extremely small populations and sampling stochasticity (Kantsa *et al.*2019). We tested the trends in the cumulative extinctions of species or of interactions during the sequential removal as proportions of the total pollinator richness or of the total interaction quantity with generalized mixed models in the *glmmTMB* package (Bates *et al.* 2015) in R (R Core Team 2017). The number of pollinator extinctions (or of interactions) was the response variable, the number of removed plant species was included as a numeric predictor and the observed/TCM/SCM was a categorical one, the total number of pollinators (or of interactions) was an Offset term (Reitan & Nielsen 2016); site identity was used as a random intercept.

In addition, we also recorded the amount of species extinctions predicted by the models that were true positives (predicted extinctions which happened in the observed networks), false positives (predicted extinctions which did not happened), true negatives (extinctions not predicted which did not happen in the observed networks) or false negatives (extinctions not predicted which did happen in reality) with both TCM and each SCM simulation at each plant removal stage.

Networks indices and beta-diversity components

We assembled interaction matrices for each stage of the experiment in all sites and calculated the following network-level indices: the binary*Connectance*, the proportion of realised links among all possible links (range 0-1); the weighted *Nestedness NODF* (Nestedness based on Overlap and Decreasing Fill) quantifies the tendency of specialized species to interact with generalists and ranges 0-100 (fully nested); the weighted *Modularity* measures the interactions partitioning into groups, it was computed by the algorithm DIRTLPAwb+ and ranges 0-1 (full compartmentalization); the weightedH_2' measures specialization based on Shannon entropy and ranges 0-1 (perfect specialisation). The following species-level indices were also calculated: the weighted*Connectivity* and *Participation*, which express the ability of a species to connect partners of different modules (*Connectivity*) or to interact with species of the same module (*Participation*). All these indices were calculated with the*rnetcarto* and *bipartite* packages for R (Dormann *et al.* 2008; Doulcier & Stouffer 2015). In addition, an index of network robustness that we name *Stochastic robustness* was calculated as the area under a curve drawn from the rate of pollinators surviving a sequential removal of all plants from the most generalist to the most specialist as simulated by 10^3 SCM (Vieira & Almeida-Neto 2015); this was

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drawn as a mean number of pollinator extinctions across simulations and was calculated separately for each experimental plant removal phase.

We quantified the turnover of interactions across the removal stages using the approach developed in Poisot *et al.* (2012). This method quantifies the total interaction turnover as $\beta_{\Omega N} = \beta_{\Sigma T} + \beta_{O\Sigma}$ and partitions it into species turnover (i.e., $\beta_{\Sigma T}$, the interaction diversity in the pool of species that are not shared between two networks) and interactions rewiring (i.e. $\beta_{O\Sigma}$, switching of interacting partners in species occurring in both networks). These were calculated for all sites and consecutive stages of the experimental removal (before - 1 sp. removed, 1 sp. removed – 2 spp. removed, and so forth) with Whittaker's beta-diversity index and its components extracted with the package *betalink* (Poisot 2016). Values for these indices range from 0 to 1; higher values indicate higher turnover or rewiring.

Two types of interaction matrix were used for the turnover analyses; one, as in Poisot *et al.* (2012), uses binary matrices and focuses on the number of interaction links per species. In addition, to account for the frequency of interactions, we also employed a quantitative version of beta-diversity that is calculated as above but in which the sum of interaction frequency per species is used instead of the number of links.

The effects of plant species removal on network indices and on beta-diversity components were tested with generalized linear mixed models (GLMM) with the *glmmTMB* package in the R environment (Bates *et al.* 2015); a given index was the response, the site identity was a random intercept, and Beta or Gaussian distributions were used depending on the response variable. For the beta-diversity components, pairs of successive removal stages were used as categorical predictor variables. For the network indices, the number of removed plants was used as numerical predictor. As in Olesen & Jordano (2002), network size (AxP, with $A =$ the number of animal species and $P =$ the number of plant species in the matrix) and the number of network interactions (the quantitative matrix sum) were included in the models in order to account for their effects on index variation over the experiment. We favoured this approach rather than the delta- or z-transformations because those can cause biases (Chagnon 2015) and they are more useful for testing departures from a random expectation (Biella *et al.* 2017), while we aimed at testing the effect of a treatment in causing specific trends (i.e. increase or decrease of an index). To compare the trend of a given index with that of the control, the values from the control site during the experiment were included as an Offset term in the GLMM.

For *Connectivity* and *Participation*, plants and pollinators were analyzed separately in GLMMs with a given index as a response variable, the number of removed plant species as numerical predictor and species identity within site as the random intercept. Here, it was not possible to include the control site for direct comparison because not all species were shared with the removal sites.

Drivers of interactions

For each site and for each plant removal stage, several simulation models were constructed from different probability matrices to explore the factors driving the observed interactions and indices. The matrices used for the models were: NULL(N) explores the effect of randomness and all species have the same probability of interactions (=1); ABUNDANCES investigates the role of abundances of either or both network levels and the matrix is filled with either the number of flowers of a plant(P), or the abundance of the pollinator species calculated as total abundance of flower visitors of that species over the entire study period (I), or the element-wise multiplication of these two $A = PxI$; (3) in MORPHOLOGICAL-MATCH(M), the matrix is filled with 1 only when a morphological match between length of insect mouthparts and a flower's nectar allocation depth occurs (Stang *et al.* 2009), for example an insect's "long-mouthparts" with a flower's "hidden-nectaries", "intermediate mouthparts" with "semi-hidden nectaries" and "short-mouthparts" with "accessible nectaries". As in Olito & Fox (2015), insects were categorized as having a long tongue (>9 mm), intermediate tongue (4-9 mm) or short (<4 mm), and plants for having nectar hidden in flower structures (e.g. larger Fabaceae and flowers with tubular corolla), semi hidden nectaries (more open tubes, smaller Fabaceae) and accessible nectaries (very short tubes or open flowers); (4) SUGAR-RESOURCES(S) assumes that the probability of interaction is proportional to amount of sugar per flower in the nectar and

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the matrix is filled with the amount of sugar/flowers per plant species (Junker *et al.* 2013); these values were obtained as detailed in Biella *et al.* (2019a) by sampling nectar from flowers bagged for 24h and with high performance anion exchange chromatography. For each matrix, probabilities were obtained by dividing the cells of the matrices by the matrix sum. In addition, the interactions of these drivers were included by building models based on multiplying two or three of the matrices described above, specifically: AxM , AxS , MxS , and $AxMxS$. We ran 10^3 simulated networks with the *mgen* function of the *bipartite* R package that distributes the interaction quantities of the real networks according to the probabilities of the model matrix. For each simulated network, network indices and beta-diversity components were calculated as for the real networks (see above). A given driver is considered as consistent with the empirical observations when its 95% confidence interval includes the real network index (Vázquez *et al.* 2009).

To investigate which of the above drivers provided the best fit in terms of predicting the occurrence and frequency of the species pairwise interactions in the observed networks, we used a likelihood approach. Following (Vázquez *et al.* 2009), a multinomial distribution was calculated from the interaction frequencies of the observed network and from a given probability matrix. Then, the delta of the Akaike information criteria (ΔAIC) was used to evaluate the ability of each probability model to predict the likelihood of pairwise interactions. As in (Vizentin-Bugoni *et al.* (2014), in the AIC calculation, the number of parameters was set as the number of species in each probability matrix multiplied by the number of matrices used in order to weight each model's complexity.

Results

The plant-flower visitor networks of the experimental sites were similar in species richness (plants P =28, pollinators I =157 in Site1; P =24, I =171 in Site2; P =20, I =106 in Site3).

Species co-extinctions

The cumulative proportion of observed and predicted extinctions increased linearly with the number of removed plants for both species and interactions ($\beta_{species}$= 0.158, likelihood ratio test $\chi^2_{plant\ removal}$= 176.356, df=1, p<0.001; $\beta_{interactions}$= 0.178, likelihood ratio test $\chi^2_{plant\ removal}$= 3838.7, df=1, p<0.001, Fig. 1). The observed networks (OBS) registered more species extinctions than the TCM and the SCM models ($\beta_{OBS-TCM}$=1.03, $\beta_{OBS-SCM}$=0.958, likelihood ratio test $\chi^2_{OBS/TCM/SCM}$=42.493, df=1, p<0.001). Similarly, the observed networks lost more interactions than what was predicted by the two models ($\beta_{OBS-TCM}$= 0.9, $\beta_{OBS-SCM}$= 0.713, likelihood ratio test $\chi^2_{observed/TCM/SCM}$= 359.1, df=1, p<0.001).

Predicted extinctions which were observed in the field (true positives) were on average (across sites and plant removal stages) the 85.33 % relative to the observed extinctions in the case of the TCM (range across sites: 33 - 100%) and were on average the 26.62 % of cases based on SCM (range: 10 – 37.7 %); the remaining predicted extinctions were not confirmed in reality (false positives). Extinctions not predicted which also did not take place in the field (true negatives) were on average 33.66% of the cases based on TCM (range 15 – 50 %) and 41.29 % based on SCM (range 10.88 – 85.53 %), the remaining proportion were extinctions not predicted which were instead observed in the field (false negatives).

Network structure and interaction turnover during plant removal

Network modularity and specialization significantly increased with the number of removed plants, while nestedness decreased significantly (Fig. 2, Table 1). However, when the values from the control site were used as an offset, the statistical significance of the increase in modularity and decrease in nestedness was confirmed, but the significance of specialization was not confirmed (Table 1). The trends of other network indices were not significant during the sequential plant removal. In the species-level indices, plants and pollinators differed in responses (Fig. 2, Table 1), where only the plant Connectivity increased significantly, while plant Participation and the pollinator indices were nearly constant during the sequential plant removal.

The interaction turnover was high in both quantitative and binary versions (Fig. 3), with a larger proportion attributable to rewiring than to species turnover; however, no statistically significant trend was found in these indices in response to the treatment (Table 1).

Drivers of network structure and interaction turnover

In the likelihood analysis (Table 2), models based on species abundance usually provided the best fit to the observed species interactions, especially in the case of the pollinator abundances model (I); the null model assuming equal probability of all interactions (NU) predicted the observed interactions as the plant removal progressed; the S model based on the amount of sugars in nectar (S) also contributed to describing the interactions (i.e. it had low ΔAIC values).

In the networks and beta-diversities (Fig. 4, and S1, S2, S3, S4 Figures), none of the models generated CI including every observed index. The *Connectance* and *H2'* were particularly poorly predicted. Remarkably, both P and I models and the multiplication of abundances with others were explaining the observed indices in multiple cases (e.g. *NODF, Modularity, WN, OS, ST*) and *MxS* predicted *NODF* in most cases. In addition, the predictors usually changed as the removal of plants progressed, such as M and S predicting both *OS* and *ST* after the first removal, and, before removal, both M predicting the *Modularity* and M with abundances predicting *H2'*. In some cases, the complexity of the models (i.e. from the multiplication of probability matrices) either increased the predicting power (*Modularity*, *NODF, WN, OS*) or decreased it (*H2'*, *ST*) as the removal progressed.

Discussion

In the networks of this study, the removal of generalist plants caused a linear decrease in nestedness, a possible symptom of instability (Burgos *et al.* 2007) because specialist species may be less entangled into the generalist pool (Jordano *et al.* 2006). Concurrently, the observed linear increase in modularity indicates an emergence of a sub-networked structure, a sign of potential network breakdown (Reis *et al.* 2014). Although compartmentalization of predator-prey food-webs is considered beneficial as it buffers against alterations spreading throughout the entire web (Stouffer & Bascompte 2011), in mutualistic networks a very high modularity actually prevents the access to alternative resources and it can be linked to decreased stability (Thébault & Fontaine 2010). Specialisation also increased during the successive plant species removal, possibly as a result of decreased pollinator abundances as previously shown by Biella *et al.* (2019a), i.e. reductions in the number of interactions triggers changes in network structure (Burkle & Knight 2012; Moreira *et al.* 2015).

Changes in nestedness and modularity did not translate into a lower stochastic robustness index. A possible reason for this relies on the dynamic yet asymmetric re-organization of species interactions along the sequence of plant removal. While the remaining plant species became increasingly centralized in the network, there was no trend in the average centralization of pollinator species. In addition, the network rewiring was high and played a larger role than species turnover in determining interaction turnover during the experiment, as in CaraDonna *et al.* (2017), although without a clear trend during the experiment. As rewiring has traditionally been associated with network stability (Kondoh 2003; Kaiser-Bunbury & Blüthgen 2015), both the observed increased plant centrality and high rewiring could explain why network robustness index increased as more plants were removed.

Many network indices were predicted by complex combinations of predictors, such as the interaction of abundances, morphological match, and sugar rewards. This was especially the case as several plants were removed, which could suggest a prominence of network complexity following the removal of generalist plants. Conversely, some of the simpler models gave good predictions of some indices, but poor predictions of others. Some remarkable positive examples are: flower abundance predicting nestedness, which reflects the role of abundant generalist plants which interact with numerous insects and drives the nested pattern (Bascompte *et al.* 2003); modularity being predicted, before plant removal, by the morphological match of corolla depth and mouthpart length, suggesting that trait matching is relevant in defining modules (Dicks *et al.* 2002; Dupont & Olesen 2009; Watts *et al.* 2016); nestedness being predicted by the interaction of morphological matching and sugar amount in the nectar, which confirms that trait matching allows an efficient resource gathering (Rodríguez-Gironés & Santamaría 2006; Balfour *et al.* 2013); network rewiring being predicted by abundances, and by the interaction of abundances and sugar amount, as the abundant and rewarding

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plants are more central in the network and more likely to establish new interactions (Jordano *et al.* 2003; Martín González *et al.*2010); morphology matching predicting the rewiring in some stages of plant removal, indicating that utilization of new resources is constrained within trait-spaces (Biella *et al.* 2019a).

On the other hand, individual pairwise interactions were explained best by the model using pollinator abundances during the entire experiment, and, when several plants were removed, by the null model assuming equal probability of interactions. The role of pollinator abundance reflects the relationship between abundance and generalization of interactions (Ollerton *et al.* 2003; Vázquez *et al.* 2009); the superior fit of the null model in the later stages of the experiment suggests an emergence of randomness in species interactions in impoverished communities. The role of randomness in ruling pairwise interactions is particularly alarming, because it would indicate the disruption of established interaction assembly mechanisms, and may also be linked to opportunism in interactions and high rewiring (Ponisio *et al.*2017).

Both species and interaction extinctions increased linearly as generalist plants were removed. As far as we know, previous studies have only used *in-silico* estimation of extinctions (Kaiser-Bunbury*et al.* 2010; Evans *et al.* 2013; Bane *et al.* 2018), but our experiment clarifies that TCM and SCM underestimated species extinction rates, and the rate of false positives and false negatives was high in relation to the identity of the species that are lost. Furthermore, these models underestimated the rate of interaction loss, which is a major flaw of currently available simulations, an issue that has been already pointed out (Santamaría *et al.* 2016). Altogether, field experiments such as the one we performed have a big potential for validating, rejecting or refining the theoretical insights gained by simulation models, and could trigger further development of more accurate models on network functioning, stability and co-extinction rates.

In conclusion, species interactions are sensitive to the extinction of generalist plants, and the rate of pollinator extinctions was similar to what is expected from network co-extinction models. When the key plants are removed, the network structure changes, extinctions of species and interactions increase, and opportunism can take place. This gives strong support to proposals indicating that conservation of interactions should be centered on the generalist species (Montoya *et al.* 2012; Biella *et al.* 2017). However, this generalist-based conservation view should consider the dynamics and re-organization of interactions and the asymmetrical responses between plants and pollinator levels, which compensate for an even more detrimental collapse of species networks.

Figure 1 – Cumulative proportion of extinctions of species and of interactions over the sequential plant removal as observed in the real networks ("OBS") and as predicted by TCM and SCM co-extinction models for each site. In SCM, the symbols and lines indicate the mean and 5%-95% quantiles of 10^3 simulations. Significances are expressed in the Results.

Figure 2 – Network indices responses to removal of generalist plants. The significances of predictors are expressed in Table 1. The black line is the average trend predicted by the models, coloured lines are predictions for each site; plots with black line only were not significant models.

Figure 3 – Interaction turnover of pairs of networks after each stage of plant removal. Both the binary indices and their quantitative counterparts are plotted. Significances of predictors are expressed in Table 1.

Figure 4 – Heatmap indicating the overlap between the observed network or beta-diversity indices and the confidence intervals of 10^3 simulations generated from probability matrices (in columns; model acronyms are described in the Methods.). Colours symbolize the number of sites being predicted correctly: red is for correct prediction in 3 sites, orange is for 2 sites and pink is for 1 site.

Supporting information

Figure S1. Network Connectance and Nestedness indices detection by probability models for each site.

Figure S2. Network Specialization and Modularity indices detection by probability models for each site.

Figure S3. Qualitative interaction turnover indices detection by probability models for each site.

Figure S4. Quantitative interaction turnover indices detection by probability models for each site.

Table 1. - Statistics of the network indices and interaction turnover components. Each row is a separate generalized mixed effect model, further details are in Methods. WN is total beta diversity, OS is the rewiring of interactions, ST is the species turnover between networks pairs. "W." stands for "weighted". ΔAIC is calculated as AIC_i - AIC_{min}. In bold the statistically significant predictors are highlighted (P<0.05). Significance of the models including the offsets with the control site's indices are given.

	Df	ΔAIC	χ^2	P	P with control offset
Connectance	1	1.274	0.726	0.394	0.719
NODF	1	6.032	8.032	**0.005**	**0.001**
Modularity	1	7.246	9.246	**0.002**	**0.007**
H2'	1	11.076	13.076	**<0.001**	0.073
Stochastic robustness	1	1.819	3.819	0.051	0.350
Connectivity plants	1	10.439	12.439	**<0.001**	NA
Participation plants	1	1.857	0.143	0.705	NA
Connectivity pollinators	1	5.285	7.285	**0.007**	NA
Participation pollinators	1	1.509	0.491	0.484	NA
WN (β)	3	0.604	5.396	0.145	0.110
OS (rewiring)	3	3.793	2.207	0.531	0.525
ST (turnover)	3	2.262	3.738	0.291	0.323
W. WN (β)	3	4.170	1.830	0.608	0.688
W. OS (rewiring)	3	2.581	3.419	0.331	0.698
W. ST(turnover)	3	1.400	4.600	0.204	0.890

Table 2 – Models' likelihood of pairwise species interactions drivers (ΔAIC). In bold, the probability models that best predicted the interactions are highlighted; the second important probability models are underlined. Model acronyms are described in the Methods.

Site	Species removed	NU	P	I	A	M	S	AxS	AxM	SxM	MxAx
Site1	0 spp.	4812.74	5218.36	**0.00**	5580.98	6752.64	707.81	7539.28	_184.16_	3004.32	2281.8
Site2	0 spp.	1539.41	1664.42	**0.00**	3079.29	2698.48	_322.79_	4176.45	1214.89	3052.62	3906.8
Site3	0 spp.	62.43	_35.79_	**0.00**	83.98	307.85	91.98	300.99	263.12	292.37	450.94
Site1	1 spp.	2304.65	2376.03	**0.00**	2564.01	3131.56	253.93	3597.58	_188.34_	1196.39	1072.5
Site2	1 spp.	817.87	1108.17	**0.00**	1525.95	1833.28	_416.13_	2614.27	1427.68	1349.81	2280.1
Site3	1 spp.	_57.07_	127.65	**0.00**	250.72	357.14	156.32	537.18	373.98	455.47	664.68
Site1	2 spp.	346.69	305.53	**0.00**	1017.21	2078.38	_95.36_	2709.90	1094.55	1165.87	1823.9
Site2	2 spp.	326.20	361.91	**0.00**	1341.76	422.59	_167.22_	1578.92	223.22	1616.49	1704.1
Site3	2 spp.	_61.12_	92.82	**0.00**	562.00	505.00	147.55	1036.19	491.58	774.95	1027.1
Site1	3 spp.	**0.00**	230.70	219.08	_143.55_	935.75	532.68	1187.56	1068.96	825.74	1062.6
Site2	3 spp.	**0.00**	163.23	_123.26_	387.34	526.63	388.07	900.07	751.48	693.46	972.02
Site3	3 spp.	97.72	**0.00**	_74.24_	520.31	701.97	88.27	1095.48	520.76	664.28	935.12

8

Site	Species removed	NU	P	I	A	M	S	AxS	AxM	SxM	MxAx
Site1	4 spp.	**0.00**	124.06	162.01	*28.97*	760.64	408.50	991.81	1023.36	650.01	973.84
Site2	4 spp.	**0.00**	155.87	*127.40*	330.28	902.66	447.01	1298.55	944.37	795.11	1023.2
Site3	4 spp.	*2.81*	**0.00**	11.59	114.62	230.76	64.75	317.72	249.87	241.70	311.29

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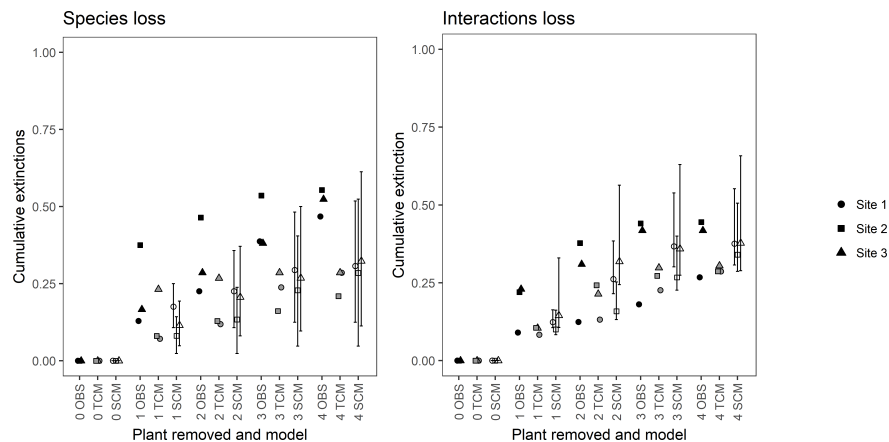
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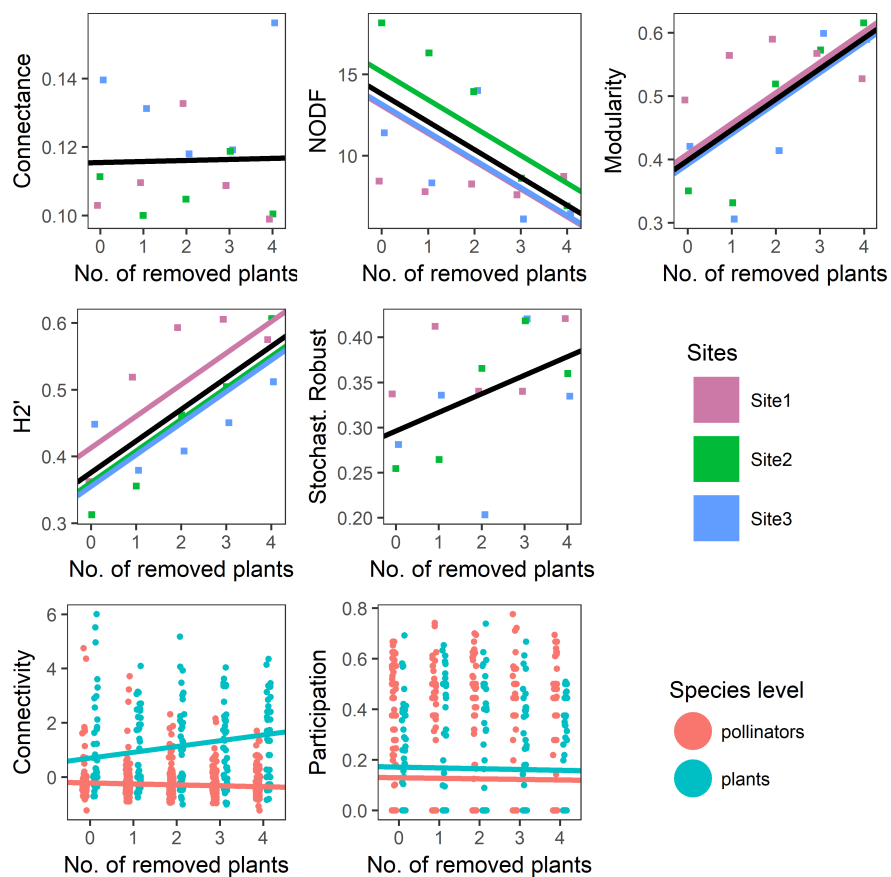
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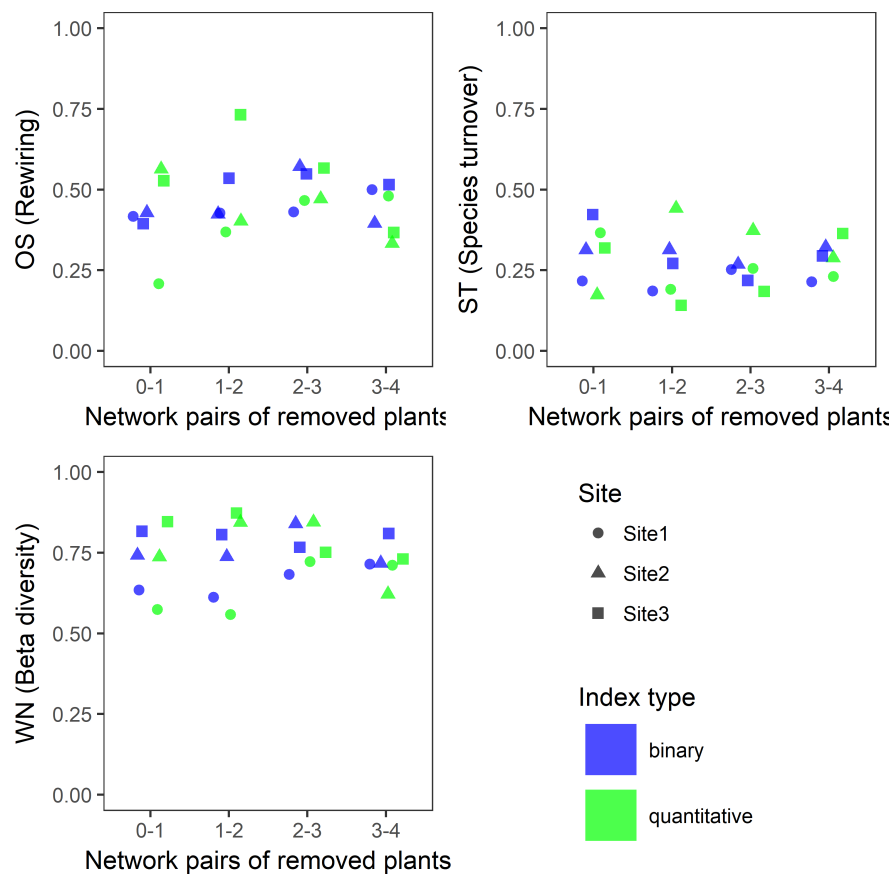
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