

Removing interactions, rather than species, casts doubt on the high robustness of pollination networks

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In the last 15 years, a complex networks perspective has been increasingly used in the robustness assessment of ecological systems. It is therefore crucial to assess the reliability of such tools. Based on the traditional simulation of node (species) removal, mutualistic pollination networks are considered to be relatively robust because of their 1) truncated power-law degree distribution, 2) redundancy in the number of pollinators per plant and 3) nested interaction pattern. However, species removal is only one of several possible approaches to network robustness assessment. Empirical evidence suggests a decline in abundance prior to the extinction of interacting species, arguing in favour of an interaction removal-based approach (i.e. interaction disruption), as opposed to traditional species removal. For simulated networks, these two approaches yield radically different conclusions, but no tests are currently available for empirical mutualistic networks. This study compared this new robustness evaluation approach based on interaction extinction versus the traditional species removal approach for 12 alpine and subalpine pollination networks. In comparison with species removal, interaction removal produced higher robustness in the worst-case extinction scenario but lower robustness in the best-case extinction scenario. Our results indicate that: 1) these two approaches yield very different conclusions and 2) existing assessments of ecological network robustness could be overly optimistic, at least those based on a disturbance affecting species at random or beginning with the least connected species. Therefore, further empirical study of plant–pollinator interactions in disturbed ecosystems is imperative to understand how pollination networks are disassembled.

Studies about robustness of complex ecological systems against disturbances have been the focus of researchers for some time (MacArthur 1955, Brodie et al. 2014). In the last 15 years, significant advances have been made with the aid of network analysis (Solé and Montoya 2001, Rezende et al. 2007, Vieira and Almeida-Neto 2015). Two main kinds of networks have been considered: one-mode networks, such as food webs (Solé and Montoya 2001), and bipartite networks, such as mutualistic interactions (Memmott et al. 2004), where two subsets of nodes (e.g. plants and pollinators) interact with each other. In both cases, studying network robustness is crucial to understand the responses of ecological communities to species extinctions (Solé and Montoya 2001) and the role of network structure in maintaining biodiversity (Dunne et al. 2002).

Ecological research on the robustness of bipartite mutualistic networks has directly imported the traditional topological robustness approach (sensu Berg et al. 2015) consisting of the simulation of node (i.e. species) removal (Memmott et al. 2004, Burgos et al. 2007, Kaiser-Bunbury et al. 2010, Astegiano et al. 2015) originally developed for one-mode networks (Albert et al. 2000, Solé and Montoya 2001, Proulx and Phillips 2005). In the case of pollination networks, recent

advances include the rewiring possibility (Kaiser-Bunbury et al. 2010), interaction strength (Kaiser-Bunbury et al. 2010, Vieira and Almeida-Neto 2015) and a merger of population dynamics and topological robustness (Fortuna and Bascompte 2006, Valdovinos et al. 2009, 2013, Ramos-Jiliberto et al. 2012). Based on the simulation of species extinctions, pollination networks are considered to be fairly robust because of their 1) truncated power-law distribution of the number of interactions per species (Jordano et al. 2003, Memmott et al. 2004); 2) asymmetry in network dimensions (redundancy in the number of floral visitors per plant – Memmott et al. 2004); and 3) nested interaction pattern (Bascompte et al. 2003, Memmott et al. 2004).

Recent findings highlight the need to shift the focus of research on ecological network robustness from species to interactions (Allesina et al. 2009, Poisot et al. 2012, Valiente-Banuet et al. 2014). Interaction extinction is likely to be fundamental in the disassembling of bipartite interaction networks, because the number of interactions is positively related to species abundance (Olesen et al. 2008, Stang et al. 2009), and plant–flower visitor interactions are lost two to three times faster than species with increasing habitat fragmentation (Sabatino et al. 2010, Burkle and Knight 2012).

The robustness of complex networks against various types of interaction removal, apart from nodes, has been little studied (Holme et al. 2002). In ecology, simulation of interaction removal has been performed for empirical food webs (Gao et al. 2006) and the distinction between redundant and functional interactions is relevant for the robustness of food webs (Allesina et al. 2009). Interaction extinction has only recently been expanded to simulated mutualistic networks by Pastor et al. (2012).

The logic underlying this approach is based on the recently appreciated fact that two species do not always interact whenever they co-occur (Poisot et al. 2012). This is true for stable communities where abundance fluctuations are within normal bounds, but for the objectives of this paper it is particularly important in situations of gradual, rather than sudden, erosion of abundance in the face of environmental degradation. In such a scenario, an interaction may disappear before any of the species involved in that interaction becomes extinct (Allesina et al. 2009, Hegland and Nielsen 2009). For example, Anderson et al. (2011) showed the importance of the functional extinction (*sensu* Dayton et al. 2000, Brodie et al. 2014) of pollinating birds in pollination networks, where interactions broke down when the density of pollinating birds fell below a threshold, without becoming extinct. Rewiring that occurs in stable communities, where no disassembly is taking place (Olesen et al. 2008, Petanidou et al. 2008) has also to be clearly distinguished from the scenario considered here, where interactions steadily disappear due to environmental degradation. Rewiring can also occur during disassembly and increase robustness (Kaiser-Bunbury et al. 2010, Ramos-Jiliberto et al. 2012) but is beyond the scope of our study.

Based on the previous available results obtained for empirical food webs (Gao et al. 2006, Allesina et al. 2009) and simulated pollination networks (Pastor et al. 2012), we expected the simulation of interaction extinctions to produce qualitatively different extinction patterns from those obtained using the node extinction approach. This would imply that the traditional approach to robustness assessment might lead to overly-optimistic conclusions about the robustness of pollination networks (Gao et al. 2006, Allesina et al. 2009, Pastor et al. 2012). Alternatively, if these two approaches produced similar results for empirical networks, assessing robustness by removing nodes would be appropriate and simpler.

The main goal of this study is to assess whether there are differences in the robustness of alpine and subalpine pollination (hereafter ASP) networks when interactions rather than species are cumulatively removed. A parallel study (Santamaría et al. 2014) evaluated the robustness of the 12 available ASP networks using the traditional approach. Here, we use the data set from that study to estimate the robustness of ASP networks to the removal of their interactions. As these two robustness assessment approaches are not directly comparable (Gao et al. 2006), we have first developed a 'common ground' between them using 1) three interaction extinction sequences representing best-, worst- and intermediate-case scenarios; 2) a conversion of interaction-based extinction plots into node extinction plots; and 3) comparable quantitative robustness indices for each robustness assessment approach. We have then asked: 1) Do different robustness

assessment approaches using the same representation (i.e. comparable plots) yield similar results? 2) What is the role of network asymmetry in the new robustness assessment approach? 3) Do the interaction-based and the node-based extinction plots yield similar results for the interaction extinction approach? This last question asks to what extent the conversion of interaction-based extinction plots into node-based extinction plots is warranted. Overall, the different approaches yield very different results, even increasing the effect of network asymmetry on robustness. We conclude, therefore, that the traditional approach to robustness assessment may lead to overly-optimistic conclusions about the robustness of pollination networks.

Material and methods

We applied the interaction extinction approach to robustness assessment recently proposed by Pastor et al. (2012) to 12 empirical binary ASP networks previously analyzed in Santamaría et al. (2014) using the traditional node (species) extinction approach (Memmott et al. 2004). Although weighted networks would be preferable, only three weighted ASP networks were available. Thus, we emphasize patterns for binary networks and address the tentative differences obtained when using an analogous weighted interaction extinction approach in the discussion.

As in the node-based robustness assessment (hereafter NBRA) approach, a species is considered extinct in the interaction-based robustness assessment (hereafter IBRA) approach when all their mutualistic interactions are lost. Contrary to NBRA, there is no distinction between primary and secondary extinctions based on subsets (plants or pollinators) of species (see Vieira and Almeida-Neto 2015 for a similar approach). Instead, the primary removal of 'interactions' produces secondary extinctions of 'nodes' in both plants and pollinators. Interaction-based removal is a generalization of node-based removal. Therefore, the comparison of robustness between NBRA and IBRA may not be straightforward (Fig. 1). We have achieved comparability by focusing on secondary extinctions of species, by means of three complementary analyses intended to: 1) establish best- and worst-case scenario extinction sequences for IBRA that could be compared with those of NBRA; 2) develop extinction plots that were directly comparable across approaches (Fig. 1); and 3) calculate indices of robustness for these extinction plots.

First, we implemented three interaction extinction sequences in IBRA intended to produce best-, worst- and intermediate case scenarios, as has been done in NBRA (Memmott et al. 2004). The first sequence always removed the interaction between the most connected species (hereafter, most connected first) and its most connected mutualistic partner. When more than one species had the same degree of connectivity, we randomly chose one of them. This process was repeated as many times as the number of interactions in the network until the last interaction (the least connected species and its least connected mutualistic partner) was removed. Note that, contrary to NBRA, interaction removal did not follow a predefined sequence because the degree of species was updated after each interaction extinction. The

subset (Fig. 1). These are the most favourable cases for each pair of symmetrical extinction curves, because these curves are the ones located above the diagonal. They allow a more direct comparison with NBRA, because interaction extinction produces faster species extinction in the largest subset than in the smallest one.

Thirdly, based on the extinction plots in NBRA, an index of robustness, R_{50} , has been proposed (Dunne et al. 2002). In a similar way, we used the bipartite R_{50} index of robustness introduced by Pastor et al. (2012) to facilitate the comparison of robustness between scenarios and networks. We refer to this index as R_{50-N-N} to indicate that it is based on the node–node extinction plot of IBRA. We introduced an analogous index named R_{50-N-I} based on the node–interaction extinction plot of IBRA calculated as the proportion of interaction extinctions necessary to cause the secondary extinction of 50% of the species in the smallest subset.

To compare robustness under NBRA (analyzed in Santamaría et al. 2014) and IBRA, we used the NBRA and the IBRA node–node extinction plots and their corresponding R_{50} and R_{50-N-N} robustness indices (Fig. 1). We specifically compared the best- and the worst-case extinction scenarios of NBRA with the best- and the worst-case extinction scenarios of IBRA respectively (see Results and Discussion about what turned out to be the best- and worst-case scenarios in IBRA). We also compared to what extent there was a match between the node–node and node–interaction extinction plots of IBRA and between their corresponding R_{50-N-N} and R_{50-N-I} indices (Fig. 1). Comparisons were carried out in two steps. First, differences in robustness values were tested by means of a paired t-test in SPSS 12.0. In the NBRA-IBRA comparison, we tested the difference $R_{50} - R_{50-N-N}$ and in the comparison between node–node and node–interaction IBRA extinction plots, we tested the difference $R_{50-N-N} - R_{50-N-I}$. We then used a Spearman’s correlation analysis in SPSS 12.0 to examine the correlation between the different robustness indices, R_{50} with R_{50-N-N} and R_{50-N-N} with R_{50-N-I} .

To compare the influence of network asymmetry on robustness across robustness indices (R_{50} , R_{50-N-N} and R_{50-N-I}), we calculated the asymmetry of each network as the $|(\text{number of pollinators} - \text{number of plants})/(\text{number of pollinators} + \text{number of plants})|$. We then correlated asymmetry with each robustness index using a Spearman’s correlation.

Data deposition

Data and computer code available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.73520>> (Santamaría et al. 2015).

Results

Comparison of node–node extinction obtained using IBRA and NBRA

Three main differences in node–node extinction were obtained using IBRA compared to NBRA. First, removing interactions between the most connected species was not always more damaging than removing interactions between species with few connections (Table 1, Supplementary material Appendix 1 Fig. A1). Secondly, differences in robustness values between extinction sequences for a given network were smaller (Table 1, Supplementary material Appendix 1 Fig. A1); and thirdly, the relationship between robustness and asymmetry was stronger (Supplementary material Appendix 2 Fig. A5).

Taking into account the proper match of best- and worst-case scenarios under IBRA and NBRA, IBRA predicted significantly higher robustness (R_{50-N-N}) than NBRA (R_{50}) in the worst-case extinction scenario and significantly lower robustness in the both the best-case and random extinction scenarios (Table 2).

Correlations between R_{50} (NBRA) and R_{50-N-N} (IBRA) were positive and significant in both the worst-case and random extinction scenarios (Table 2).

Table 1. Proportion of primary species (R_{50} and R_{50-N-N}) or interactions (R_{50-N-I}) that need to be removed to incur in $\geq 50\%$ of secondary species extinctions for the three interaction extinction sequences simulated in the 12 ASP networks.

| | Asymmetry | Most-to-least | Most connected first | | Least-to-most | Least connected first | | Random | | |
|--|-----------|---------------|----------------------|--------------|---------------|-----------------------|--------------|----------|--------------|--------------|
| | | R_{50} | R_{50-N-N} | R_{50-N-I} | R_{50} | R_{50-N-N} | R_{50-N-I} | R_{50} | R_{50-N-N} | R_{50-N-I} |
| Abisko (Elberling and Olesen 1999) | 0.67 | 0.82 | 0.91 | 0.96 | 0.99 | 0.87 | 0.68 | 0.94 | 0.86 | 0.93 |
| Arthur’s Pass (Primack 1983) | 0.51 | 0.73 | 0.84 | 0.93 | 0.99 | 0.82 | 0.69 | 0.96 | 0.80 | 0.90 |
| Cerro Franciscano (Arroyo et al. 1982) | −0.19 | 0.24 | 0.66 | 0.86 | 0.95 | 0.37 | 0.33 | 0.73 | 0.53 | 0.73 |
| Craigieburn (Primack 1983) | 0.15 | 0.64 | 0.64 | 0.93 | 0.99 | 0.71 | 0.55 | 0.89 | 0.63 | 0.89 |
| Farellones (Arroyo et al. 1982) | 0.06 | 0.30 | 0.56 | 0.89 | 0.99 | 0.62 | 0.36 | 0.80 | 0.58 | 0.80 |
| La Parva (Arroyo et al. 1982) | 0.18 | 0.37 | 0.66 | 0.90 | 0.99 | 0.67 | 0.45 | 0.84 | 0.63 | 0.83 |
| Lagunillas (Ramos-Jiliberto et al. 2010) | 0.18 | 0.36 | 0.65 | 0.90 | 0.98 | 0.69 | 0.41 | 0.83 | 0.63 | 0.83 |
| Mount Cook (Primack 1983) | 0.53 | 0.49 | 0.85 | 0.94 | 0.99 | 0.88 | 0.70 | 0.91 | 0.79 | 0.90 |
| Picos de Europa (current study) | 0.19 | 0.59 | 0.66 | 0.96 | 1.00 | 0.70 | 0.40 | 0.94 | 0.65 | 0.93 |
| Rocky Mountain (Burkle and Irwin 2009) | −0.04 | 0.51 | 0.55 | 0.95 | 0.99 | 0.40 | 0.26 | 0.91 | 0.49 | 0.91 |
| Sierra Nevada (current study) | 0.56 | 0.61 | 0.86 | 0.97 | 1.00 | 0.87 | 0.69 | 0.96 | 0.83 | 0.96 |
| Teide (Dupont et al. 2003) | 0.55 | 0.74 | 0.87 | 0.96 | 0.98 | 0.85 | 0.79 | 0.94 | 0.83 | 0.94 |

Table 2. Average \pm SD differences in robustness ($R_{50} - R_{50-N-N}$) between NBRA and IBRA for the three extinction sequences. The results of the paired t-test (t) for differences in robustness and the Spearman correlation coefficient (R_s) between R_{50} and R_{50-N-N} are also shown.

| Extinction sequence | Average \pm SD | t | p | R_s | p |
|---------------------|------------------|-------|--------|-------|-------|
| Worst-case | -0.17 ± 0.15 | -4.00 | 0.002 | 0.67 | 0.018 |
| Best-case | 0.26 ± 0.13 | 7.02 | <0.001 | 0.14 | 0.660 |
| Random | 0.20 ± 0.09 | 7.42 | <0.001 | 0.70 | 0.012 |

Comparison of node–node and node–interaction extinction plots using IBRA

The robustness derived from node–interaction extinction plots was always lower for the least connected first interaction extinction sequence than for the most connected first sequence, and differences between extinction sequences were greater than those derived from node–node extinction plots (Table 1, Supplementary material Appendix 1 Fig. A2). The robustness derived from node–interaction extinction plots was also significantly higher than that derived from node–node extinction plots in the most connected first and random sequences and significantly lower in the least connected first sequence (Table 3).

The robustness derived from node–node extinction plots was positively and significantly correlated to that derived from node–interaction extinction plots for least connected first and random sequences (Table 3). No significant correlation was found between R_{50-N-N} and R_{50-N-I} in the most connected first sequence (Table 3).

Differences in robustness between subsets in the node–interaction extinction plots increased with asymmetry, although less markedly than in node–node extinction plots (Supplementary material Appendix 2 Fig. A5). When both subsets (plants and pollinators) were considered together in the node–interaction extinction plots, intermediate robustness values were obtained compared to those obtained when each subset was considered separately (Supplementary material Appendix 1 Fig. A2).

Discussion

As complex network tools have been increasingly used in the last 15 years to assess the robustness of ecological systems to disturbances affecting ecological interactions (Solé and Montoya 2001, Memmott et al. 2004, Gao et al. 2006,

Table 3. Average \pm SD differences in robustness ($R_{50-N-N} - R_{50-N-I}$) between node–node and node–interaction extinction plots of IBRA for the three extinction sequences. The results of the paired t-test (t) for differences in robustness and the Spearman correlation coefficient (R_s) between R_{50-N-I} and R_{50-N-N} are also shown.

| Extinction sequence | Average \pm SD | t | p | R_s | p |
|-----------------------|------------------|-------|--------|-------|--------|
| Most connected first | -0.20 ± 0.12 | -6.05 | <0.001 | 0.54 | 0.072 |
| Least connected first | 0.18 ± 0.08 | 4.53 | 0.001 | 0.90 | <0.001 |
| Random | -0.19 ± 0.10 | -6.77 | <0.001 | 0.65 | 0.021 |

Allesina et al. 2009, Vieira and Almeida-Neto 2015), it is crucial to assess their reliability. Previous work with simulated pollination networks suggests that different approaches radically affect the qualitative and quantitative conclusions drawn (Pastor et al. 2012). The results obtained in this study through the comparison of NBRA and IBRA based on empirical networks has two main implications in this field of research: 1) different approaches yield very different qualitative conclusions; and 2) existing topological assessments of ecological network robustness could be overly optimistic quantitatively, at least those based on disturbances affecting species at random or beginning with the least connected species.

Main differences between IBRA and NBRA and their practical implications

In the NBRA approach, the least-to-most connected sequence has been commonly considered the best possible scenario in terms of robustness, while the most-to-least connected sequence has been considered the worst (Memmott et al. 2004). To our surprise, the opposite occurs for interaction removal, i.e. the highly connected first sequence turned out to be a best-case extinction scenario and vice versa. The node–node extinction plots of IBRA resulted in significantly lower robustness when interactions, rather than species, removal initially affected the most connected species, and higher robustness when interaction removal initially affected the least connected species (Table 2, Supplementary material Appendix 1 Fig. A1–A2). In other words, whilst in NBRA the primary removal of low-degree species caused fewer secondary extinctions than the primary removal of high-degree species, in IBRA, where there is no distinction between primary and secondary extinctions, the removal of interactions between low-degree species of both plants and pollinators caused more secondary extinctions than the removal of interactions between high-degree species.

Another qualitative difference between NBRA and IBRA was that node–node extinction plots of IBRA produced very similar curves for the different extinction sequences (Table 1, Supplementary material Appendix 1 Fig. A1). To understand this difference it is important to realize that the node–node extinction plots of IBRA actually depict the relationship between plant and pollinator persistence throughout the same underlying interaction extinction process. Thus, IBRA showed a similar relationship in the rate of plant and pollinator persistence across extinction sequences. Furthermore, node–node extinction plots of IBRA were strongly influenced by network asymmetry (Supplementary material Appendix 2 Fig. A5). As the same number of interactions was divided between the two subsets, both species subsets in symmetric networks became extinct at the same rate and, therefore, both extinction curves followed the diagonal $y = 1 - x$ (Supplementary material Appendix 2 Fig. A6). However, asymmetric networks produced extinction curves above the diagonal, because the first interaction extinctions only affected species from the largest subset (Supplementary material Appendix 2 Fig. A6). The greater the asymmetry, the longer the delay in the beginning of species extinction in the smallest subset (Supplementary material Appendix 2 Fig. A6).

The observed qualitative and quantitative differences between NBRA and IBRA in the node–node extinction plots have some practical implications. The similarity in robustness across extinction sequences using IBRA downplays the importance of determining whether more connected (generalist) or less connected (specialist) species are more likely to become extinct in natural communities. Furthermore, the broad range of robustness values obtained using IBRA highlights the high dependence of robustness on the structural properties of each network (Dunne et al. 2002, Gao et al. 2006, Allesina et al. 2009, Pastor et al. 2012), which prevents generalizations about the robustness of pollination networks. As previously suggested (Memmott et al. 2004, Dormann et al. 2009, Pastor et al. 2012, Santamaría et al. 2014), network asymmetry is a key feature in the robustness of bipartite networks, which will probably determine which subset is the least robust.

Comparison of network robustness using node–node versus node–interaction extinction plots contributed to a better understanding of the interaction extinction process and clarifies why what we expected to be the best and worst-case scenarios was incorrect. The low robustness predicted from the removal of interactions between the least connected species as compared with removing interactions between the most connected species was much more obvious in the node–interaction extinction plots, where the difference in robustness between sequences was greater (Table 1, Supplementary material Appendix 1 Fig. A2). The lower robustness of the least connected first sequence in comparison with most connected first sequence is because the probability of choosing non-redundant interactions was greater when extinction began with specialist species interactions. In this way, the least connected first sequence in IBRA was actually equivalent to a sequence that began by removing the least redundant interactions, leading to the loss of the two species involved (plant and pollinator) and producing a worst-case scenario. The slope of this extinction curve increased with the proportion of species with degree one on the y-axis. Blüthgen et al. (2008) suggest that the proportion of specialist–specialist interactions may be underestimated in pollination networks. This adds relevance to the low robustness found for this sequence of interaction removal. The most connected first sequence began by removing the redundant interactions *sensu* Allesina et al. (2009), which delays the beginning of species extinction, i.e. a best-case scenario. The random sequence produced an intermediate species extinction rate, which could be diminished by nestedness, as it means that specialist–generalist interactions are the most abundant (Bascompte et al. 2003).

The low robustness to removal of interactions between species with few connections also has practical implications. It is widely assumed that disturbances affecting species with few connections will have a low impact on the network because specialists tend to interact mostly with generalists (Bascompte et al. 2003). Our results, however, indicate that the removal of a very small fraction of specialist species interactions could suffice to cause the extinction of more than 50% of species in the network (Table 1, Supplementary material Appendix 1 Fig. A2). Thus, although in a scenario of species removal nestedness protects the network from extinction of species with few connections (Burgos et al. 2007),

this does not happen in a scenario of interaction removal. The results for the least connected first interaction extinction sequence agrees with results reported for food webs (Allesina et al. 2009), suggesting that pollination networks may be potentially vulnerable to the loss of non-redundant interactions.

Need for empirical data

The significant correlation between robustness indices of node–interaction and node–node extinction plots of IBRA (Table 3) supports the use of the node–node extinction plot of IBRA as a common ground to compare NBRA and IBRA, at any rate for least connected first and random sequences. This partial match between approaches raises the question of assessing which of them, if either, is the most useful. The convenience of each approach might depend on the type of disturbance causing network disassembly. A sudden large disturbance could trigger immediate species extinctions as described by NBRA, especially if species extinction begins with the most connected species as reported by Pauw (2007). However, more gradual disturbances could first decrease species abundance and then lead to extinctions, which would be better described by IBRA, especially by the least connected first and random sequences. Such decreases in abundance causing functional extinction could be seen as a “relaxation time” (Diamond 1972) or an “extinction debt” (Brodie et al. 2014) before species extinction.

If functional extinction turns out to be a general trend in the disassembling of ecological networks, current assessments of ecological network robustness could be too optimistic, and the interaction extinction based approach would be desirable. Thus, empirical data are urgently needed. For example, including interaction diversity in the study of plant population responses to habitat fragmentation would shed light on which robustness approach is more reliable. Unfortunately, this has rarely been studied (Aguilar et al. 2006, Hadley and Betts 2012). Studies for whole communities are also scarce (Sabatino et al. 2010, Burkle and Knight 2012). Nevertheless, some evidence has been found of a decrease in population abundance preceding species extinction for food webs (Säterberg et al. 2013). In addition, mutualism failure occurs below a population abundance threshold (functional extinction threshold), even though no species is yet extinct (Bosch and Waser 2001, Anderson et al. 2011). Evidence exists too for species extinction mediated by the disruption in mutualism (Bond 1994). Increasing the mechanistic understanding of the functional extinction in pollination networks is crucial (Valiente-Banuet et al. 2014). For example, when one species decreases in abundance do all its interactions with other partners decrease in parallel or not? Are weak interactions affected more or less than strong interactions?

Limitations and further developments

Although our study provides new insights into the robustness assessment of pollination networks, we should also consider two limitations. First, a larger set of networks would improve the reliability of the statistical comparisons between approaches, even though it would not change the striking qualitative differences in robustness range obtained using the

two extinction approaches and their connection with network structure (see Dunne et al. 2002 for a similar reasoning). Secondly, considering the impact of each interaction (i.e. the benefit of plant rewards for the pollinator and pollinator effectiveness – Vázquez et al. 2012, King et al. 2013, Vieira and Almeida-Neto 2015) would have been desirable. Unfortunately, gathering such data at a network scale is a daunting task.

Additionally, our approach is a first step that can be expanded in at least four ways. First, we have focused on topological network robustness to the simulated extinction of its components. A parallel research line which evaluates the temporal persistence of species in the network by simulating population dynamics is a complementary tool that can shed light on how species abundance fluctuation affects current inferences on bipartite network structure and robustness (Fortuna and Bascompte 2006, Valdovinos et al. 2009, 2013, Ramos-Jiliberto et al. 2012, García-Algarra et al. 2014, Vázquez et al. 2015). It is also extremely important to obtain empirical information on how ecological networks are disassembled, following the lead of Sabatino et al. (2010) and Burkle and Knight (2012). These two approaches should be merged in future studies.

Secondly, the possibility of rewiring should also be incorporated into IBRA as it has been done in NBRA (Kaiser-Bunbury et al. 2010, Ramos-Jiliberto et al. 2012). We are aware that assuming that a species losing all its interactions cannot rewire to other species and inevitably becomes extinct is too constrained. However, available empirical evidence on pollinator behaviour is insufficient to establish realistic rewiring rules either in NBRA and IBRA. We expect that rewiring may increase robustness in IBRA as it does in NBRA (Kaiser-Bunbury et al. 2010, Ramos-Jiliberto et al. 2012) without changing qualitatively our conclusions.

Thirdly, how to achieve a proper comparison between IBRA and NBRA needs further consideration. Despite rapid progress on the simulation of ecological network disassembly, there is a lack of comparisons between the results of different methods. This may be partly because the absence of comparability between them (Gao et al. 2006, Kaiser-Bunbury et al. 2010). We have tried to develop a common ground between NBRA and IBRA but we are aware of its limitations. The IBRA sequences proposed in this study are analogous to those of NBRA in the sense that they indicate best- and worst-case extinction scenarios. Our choice covered the two most extreme scenarios, but finding exact analogues to NBRA extinction sequences is complex, thus hindering the comparability of NBRA and IBRA. Of course, other interaction extinction sequences are possible. Any other potential interaction extinction sequence would be intermediate between the ones modelled here and, although possibly more easily comparable with NBRA, would be less informative. In the absence of empirical evidence of how pollination networks disassemble, exploring the most extreme extinction scenarios seems more desirable and represents a valuable step forward in the assessment of network robustness, by providing a sound base for generalization of the NBRA. Our extinction sequences allow us to explore what happens when the interaction removal is preferably directed to the most- or least-redundant interactions (in the spirit of Allesina et al. 2009). Our initial consideration of best- and worst-case

scenarios was incorrect and a proper interpretation required us to pay attention to the functionality or redundancy of the interactions removed. Although we did not specifically test it, choosing less extreme interaction extinction sequences could avoid the reversal in the ranking of robustness of the extinction sequences compared to NBRA. Consideration of these less extreme extinction sequences could improve the comparability between NBRA and IBRA and deserves future consideration.

Finally, interaction frequency could be taken into account, either directly or through interaction strength (Gilarranz et al. 2012, Vázquez et al. 2012, Vieira and Almeida-Neto 2015). We have tentatively explored the effects of interaction frequency incorporation using the three ASP networks for which interaction frequency data were available. We simulated three analogous sequences of interaction extinction using interaction frequency as our decision criterion of interaction selection to be removed (Supplementary material Appendix 2 Fig. A5–A6). In this case, the most-to-least sequence removed interactions from the most to the least frequent, and the least-to-most sequence removed interactions from the least to the most frequent. We found important differences between this approach and the qualitative ones. As the three networks showed different responses to the same weighted interaction extinction sequences, general conclusions cannot be made. However, we noticed that when the least frequent interactions were removed first, species from the largest subset – which had a higher proportion of rare interactions – became extinct faster than species from the smallest subset. This result suggests that asymmetry may also be a key structural pattern in the weighted interaction extinction approach, at least for the least-to-most sequence. The apparently higher robustness in the least-to-most sequence of weighted IBRA compared to un-weighted IBRA could be explained by the asymmetry of dependence (Bascompte et al. 2006) or simply by the high proportion of rare interactions that introduced randomness in the interaction extinction order. Incorporation of interaction strength also leads to increases or decreases in robustness in recent analyses (Vieira and Almeida-Neto 2015). Since our weighted interaction extinction approach yielded promising results, a comparison between weighted and un-weighted interaction extinction approaches deserves further research using a larger set of weighted networks.

Conclusion

Our comparison of the whole range of network robustness produced by different scenarios of disassembly showed that network robustness was very dependent on the approach used. In general, the interaction extinction approach yielded a greater effect of asymmetry and low robustness to the extinction of interactions between the least connected species. Although we only had three alpine weighted networks, our results also revealed differences between weighted and un-weighted interaction extinction assessment approaches. Furthermore, network asymmetry influenced all approaches (node-based, interaction-based and weighted interaction-based) to a different extent. Thus, we are still far from understanding the robustness of alpine and subalpine (and probably other) pollination networks. These differences

between approaches highlight the need to empirically document which of them (if any) is the most suitable. We need to increase our understanding of empirical plant–pollinator interactions in disturbed ecosystems to increase the realism of simulated scenarios of robustness assessment.

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Supplementary material (available online as Appendix oik-02921 at <www.oikosjournal.org/appendix/oik-02921>). Appendix 1–2.