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Robustness of alpine pollination networks: effects of network structure and consequences for endemic plants

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Abstract

Global threats to plant-pollinator interactions are potentially serious in alpine ecosystems, which combine great diversity with particular fragility. We utilized tools from complex network theory to assess the robustness to species extinction of two Spanish alpine pollination networks. A comparison with ten additional alpine and subalpine pollination (ASP) networks allowed us to give our assessment a broader scope and provide a general view of ASP network robustness. We found a broad range of robustness among ASP networks. The two Spanish pollination networks ranked intermediate to high in robustness. This could be due to two of their structural features, connectance (proportion of potential interactions actually observed) and asymmetry (normalized difference between pollinator and plant richness), which showed a positive relationship with network robustness. A finer-scale focus on the two Spanish networks did not reveal differences between endemic and nonendemic plants in their functional role within the network but indicated that they differed in their robustness to pollinator extinction. Contrasting patterns across networks suggested that endemic robustness depends on community particularities. To improve the utility of robustness assessment as a conservation tool, we should increase our understanding on (1) the order in which network species will get extinct, (2) how species rewire once they have lost their partners, and (3) how much species depend on their mutualistic interaction.

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Introduction

Alpine ecosystems show a great biological diversity due to habitat heterogeneity associated with elevation gradients and topographic particularities (Körner, 2003). Furthermore, the complex history of geographic isolation of the mountains makes them reservoirs of a large number of relict and endemic groups (Kessler, 2000). However, alpine ecosystems are also particularly fragile because of the combination of extreme climatic conditions, short growing seasons, steep slopes and shallow ground. Indeed, several threats to alpine ecosystems have been suggested (Franzén and Molander, 2012).

Pollen limitation of plant reproduction is of particular concern in alpine ecosystems owing to a poor and variable pollinator service (Arroyo et al., 1982, 1985; Elberling and Olesen, 1999; Gómez and Zamora, 1999; Dupont et al., 2003). These ecosystems, thereby, are not free from the major global threats to plant-pollinator interactions such as habitat fragmentation (Aizen and Feinsinger, 1994; Olesen and Jain, 1994; Cranmer et al., 2011), biological invasions (Traveset and Richardson, 2006; Koen et al., 2012), and climate change–induced phenological mismatches between plants and pollinators (Memmott et al., 2007; Rafferty and Ives, 2011). In particular, direct and indirect evidence for effects of climate change on plant-pollinator interactions in alpine ecosystems is increasing (Wilson et al., 2005; Giménez-Benavides et al., 2007; García-Camacho and Escudero, 2009; Green, 2010; Forrest and Thomson, 2012).

Animal-pollinated plants and their pollinators are connected through direct and indirect interactions in a complex network. Therefore, plant-pollinator interaction networks (pollination networks) may provide suitable tools to address the effects of disturbances on these communities (Tylianakis et al., 2010; Devoto et al., 2012; Pocock et al., 2012). An increasingly popular way to quantifying the effect of disturbances on networks has been the assessment of network robustness to the loss of interacting species (Memmott et al., 2004; Fortuna and Bascompte, 2006; Burgos et al., 2007; Devoto et al., 2007; Memmott et al., 2007; Pauw, 2007; Kaiser-Bunbury et al., 2010; Memmott et al., 2010). The most common approach consists in simulating species extinction in empirical qualitative (i.e., based on presence/absence of interaction) networks (Memmott et al., 2004). If data about frequency of the interactions are available, more sophisticated assessments of robustness are possible (Kaiser-Bunbury et al., 2010; Pocock et al., 2012).

Pollination networks are considered to be robust to species extinction, particularly if such extinction occurs at random or hits first the least linked species in the network. This pattern holds for networks where only interaction presence/absence (Memmott et al., 2004) or interaction frequency (Kaiser-Bunbury et al., 2010) data are available. High robustness is considered to be caused by some structural patterns of pollination networks such as asymmetry and nestedness. Network asymmetry is calculated as the normalized difference between the number of pollinators minus the number of plants (Blüthgen et al., 2007). Most often, each plant in the network is connected with a high number of pollinators, and this redundancy increases network robustness to pollinator extinction (Memmott et al., 2004). Network nestedness means that generalist species interact mainly with each other and specialist species interact mainly with generalist species (Jordano et al., 2003). Nestedness

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is considered to buffer against cascading extinctions after the extinction of either specialist or generalist species (Memmott et al., 2004; see, however, Burgos et al., 2007). Nevertheless, recent empirical (Pauw, 2007) and simulation (Pocock et al., 2012) data suggest that pollination networks are either not very robust or less robust than other ecological networks.

Empirical data on the robustness of pollination networks exist (Memmott et al., 2004; Kaiser-Bunbury et al., 2010) but are too scarce to provide a general assessment such as the one carried out for food webs (Dunne et al., 2002) or comensalistic networks (Piazzon et al., 2011). Information about a larger number of pollination networks is highly desirable to increase generality of current views of network robustness and as a reference for comparison of single case studies. Furthermore, no attempt has been made to assess the robustness of specific subsets of pollination networks such as endemic plant species. Although endemic plants are often of conservation concern, they could be rather robust to pollinator extinction because it has been suggested that mountain-restricted plants often show generalist pollination systems (Olesen and Jordano, 2002). Many complex networks consist of so-called modules, i.e., groups of species that interact significantly more between them than with species from other groups (Olesen et al., 2007). Based on the distribution of the interactions within and outside their module, Olesen et al. (2007) categorized species into four topological roles: (a) module hubs, important to keep cohesion within modules, (b) connectors, important to keep cohesion between modules, (c) peripherals, with few interactions, both within and between modules, and (d) network hubs, important for holding together the structural integrity of the whole network. Roles differ in their overall connection to the network and, thus, in the effect of their extinction on network robustness (Olesen et al., 2007). By examining the distribution of roles and the differences in robustness among endemic, as compared to nonendemic, plant species, it is possible to assess their effect on network robustness and their relative vulnerability.

The aim of this study is to determine the robustness of two alpine pollination networks, considering the influence of network structure on robustness, and compare the robustness of endemic and nonendemic plants. We had four specific objectives. First, we assessed the robustness to species extinction of two Spanish alpine pollination networks. To put this assessment into a broader context, we gathered information about the robustness for ten additional alpine and subalpine pollination (ASP) networks from different regions. Second, using our data set of 12 ASP networks, we evaluated the effect of two structural features—connectance and asymmetry—on robustness. Third, for the two Spanish ASP networks, we evaluated whether there are differences between endemic and nonendemic plants in their role within the network and in their robustness to pollinator extinction. Fourth, we identified a list of caveats that must be addressed to improve the utility of robustness assessment in pollination networks.

Materials and Methods

We assessed the robustness of two alpine pollination networks located in northern Spain (Picos de Europa National Park), and southern Spain (Sierra Nevada National Park). (See Table 1 for habitat and structure description.) In order to put our assessment into context, we compared these robustness values with those of the other 10 published alpine and subalpine pollination (ASP) networks for which qualitative (binary) data are available (to our knowledge) (Table 1). We are aware that interaction frequency should be considered in the assessment of network robustness. However, the number of available ASP networks with quantitative data for such comparisons is currently too scarce.

Following Memmott et al. (2004) we evaluated network robustness by drawing extinction curves, in which the proportion of "secondary extinctions" caused by the accumulation of simulated "primary extinctions" among their mutualistic partners is represented. A species was considered extinct when all their mutualistic partners had been lost. Although Memmott et al. (2004) focused on secondary extinctions of plants as a function of the percentage of simulated extinction of pollinators; we also simulated the secondary extinction of pollinators as a function of the simulated extinction of plants. We simulated the three sequences of species extinction proposed by Memmott et al. (2004): (i) ordered extinction from the most-linked to the least-linked species (*most-to-least linked*), (ii) ordered extinction from the least-linked to the most-linked species (*least-to-most linked*), and (iii) random extinction. Following Ramos-Jiliberto et al. (2012), 300 iterations were averaged for each extinction curve. MatLab software was used for the simulation of extinction sequences (see Pastor et al., 2012, for details).

In order to quantify network robustness comparison we calculated the robustness index R_{50} from the extinction curves. Originally developed to evaluate the robustness of food webs, R_{50} is the fraction of species that has to be removed in order to result in a loss of ≥50% of species (Dunne et al., 2002). As applied to pollination networks, we calculated two values for each network: (i) robustness to pollinator extinction, that is, the fraction of primary extinctions of pollinators that has to occur in order to result in ≥50% of secondary extinction of plants, and (ii) robustness to plant extinction, that is, the fraction of primary extinctions of plants that has to occur in order to result in ≥50% of secondary extinction of pollinators. In this adaptation to pollination networks, R_{50} ranges from 1 (maximum robustness) to 1 ÷ the number of pollinators (minimum robustness to pollinator extinction) or 1 ÷ the number of plants (minimum robustness to plant extinction) (Pastor et al., 2012; Ramos-Jiliberto et al., 2012).

We assessed the influence of two structural features of the 12 ASP networks, connectance C and asymmetry D, on network robustness, using a Pearson's correlation analysis in SPSS 12.0 (Norušis, 2004). C was calculated, according to Jordano (1987), as the percentage of realized interactions between plants (P) and pollinators (A) out of the P × A potential interactions in the network. D was calculated as (A – P) ÷ (A + P) (Blüthgen et al., 2007). Thus, we correlated (i) robustness to plant or pollinator extinction and the asymmetry (D) and (ii) robustness to plant or pollinator extinction and connectance (C). In addition, we calculated the correlation between D and the difference between robustness to plant and pollinator extinction.

We used Netcarto software (Guimerà and Amaral, 2005) and the thresholds suggested by Olesen et al. (2007) to identify the topological roles (i.e., module hub, connector, peripheral, or network hub) of endemic and nonendemic plants in the Picos de Europa and Sierra Nevada pollination networks. We tested if there were differences in the frequency distribution of endemic and nonendemic plants across roles by means of a Freeman-Halton extension of the Fisher exact probability test in the SISA-Binomial website (www.quantitativeskills.com/sisa/statistics).

To assess the relative robustness of endemic and nonendemic plants to pollinator extinction, we modified the function *second. extinct* in the bipartite package in R (Dormann et al., 2008) to draw separate secondary extinction curves for endemic and nonendemic

TABLE 1

Alpine and subalpine pollination networks and their main structural features: number of species (S), number of pollinator species (A), number of plant species (P), asymmetry in network dimensions (D), number of interactions (I), and connectance (C). Marked networks (*) are published in the NCEAS interaction webs database (http://www.nceas.ucsb.edu).

Network	Habitat	S	A	P	D	I	C	Reference
Abisko	Subartic alpine community in Latnjajaure, N Sweden (985 m).	141	118	23	0.67	238	8.77	Elberling and Olesen (1999)*
Arthur's Pass	Subalpine grassland and scrub into Arthur's Pass National Park, New Zealand (900 m.).	90	68	22	0.51	147	9.83	Primack (1983)
Cerro Franciscano	Andean subnival zone in the Mediterranean sector of central Chile (3200–3600 m).	69	28	41	–0.19	91	7.92	Arroyo et al. (1982)*
Craigieburn	Subalpine grassland and rocky cliffs above the treeline used by the Craigieburn Mountains, New Zealand (1600–1800 m).	122	70	51	0.15	323	8.87	Primack (1983)
Farellones	Subandean scrub in the Mediterranean sector of central Chile (2200–2600 m).	185	98	87	0.06	372	4.36	Arroyo et al. (1982)*
La Parva	Andean semi-woody cushion scrub and perennial herbs zone in the Mediterranean sector of central Chile (2700–3100 m).	105	62	43	0.18	199	7.46	Arroyo et al. (1982)*
Lagunillas	Subandean scrub in the Mediterranean sector of central Chile (1800–2200 m).	187	110	77	0.18	362	4.27	Ramos-Jiliberto et al. (2010)
Mount Cook	Subalpine grassland and scrub in Mount Cook National Park, New Zealand (1100 m).	132	101	31	0.53	248	7.92	Primack (1983)
Picos de Europa	Temperate alpine scree, moraine and subalpine grassland in Picos de Europa National Park, Spain (2050–2100 m).	227	134	91	0.19	1197	9.64	Current study
Rocky Mountain	Alpine tundra in Rocky Mountains in Gothic, Colorado, U.S.A. (2900 m).	73	35	38	–0.04	337	25.34	Burkle and Irwin (2009)
Sierra Nevada	Mediterranean alpine grassland and scree in Sierra Nevada, Spain (2850 m).	147	115	33	0.56	544	14.78	Current study
Teide	Subalpine desert within a volcanic caldera of Tenerife, Spain (2000 m).	49	38	11	0.55	106	25.36	Dupont et al. (2003)*

plants from our three extinction sequences of primary extinctions of pollinators. We carried out 300 iterations and averaged them for each extinction curve. For the Picos de Europa network, we considered as endemic those species and subspecies with a distribution limited to Cantabrian range and Pyrenees (Castroviejo, 1986–2012). For the Sierra Nevada network, we considered as endemic those species and subspecies with a distribution limited to Sierra Nevada (Blanca et al., 2011).

In order to test for differences in the robustness to pollinator extinction between endemic and nonendemic plants for each extinction sequence, we used the 300 iterations as replicates and performed a two-way general linear model (GLM) in R, considering the factors endemism (endemic vs. nonendemic) and site (Picos de Europa vs. Sierra Nevada). We chose a binomial error distribution and a logit link function. Significantly different average robustness across treatments was identified by means of an a posteriori Tukey Honest Significant Differences test. The sequence least-to-most linked could not be analyzed this way because no variation between iterations was found. Thus, interpretation of differences in R_{50} in this case was based on visual inspection only. Because of binomial error distribution requires entire numbers, we multiplied R_{50} values by 100.

Results

ROBUSTNESS TO PLANT OR POLLINATOR EXTINCTION AND ITS RELATION TO NETWORK PROPERTIES

Both case-study networks showed values of robustness to pollinator extinction between 0.59 and 1.00 and values of robustness to plant extinction between 0.40 and 1.00 (Table 2 and Fig. A1). For the set of 12 ASP networks analyzed, robustness was dependent on the extinction sequence and the identity of the primary extinct group. Thus, network robustness decreased in the order least-to-most linked > random > most-to-least linked, and ASP networks were more robust to the extinction of species from the richest group, usually pollinator species (Table 2 and Fig. A1).

For the set of 12 ASP networks analyzed, robustness to plant extinction increased with network connectance for the most-to-least linked sequence (Fig. 1 and Table A1). No other significant relationship between network robustness and network connectance was found (Table A1). Robustness to pollinator extinction increased with network asymmetry for the most-to-least linked and random sequences (Fig. 1 and Table A1). No other significant relationship between network

TABLE 2

Robustness (R_{50}) to the three sequences of pollinator and plant extinction in the 12 alpine and subalpine pollination networks studied. Most-to-least linked: extinction starts in the most connected species; least-to-most linked: extinction starts in the least connected species; random: extinction of species at random.

	Extinction sequence					
	Most-to-least linked		Least-to-most linked		Random	
	Robustness to pollinator extinction	Robustness to plant extinction	Robustness to pollinator extinction	Robustness to plant extinction	Robustness to pollinator extinction	Robustness to plant extinction
Abisko	0.82	0.30	0.99	0.89	0.94	0.64
Arthur's Pass	0.73	0.37	0.99	0.85	0.96	0.69
Cerro Franciscano	0.20	0.24	0.97	0.95	0.68	0.73
Craigieburn	0.64	0.57	0.99	0.94	0.89	0.83
Farellones	0.30	0.30	0.99	0.95	0.80	0.74
La Parva	0.37	0.39	0.99	0.95	0.84	0.75
Lagunillas	0.36	0.34	0.98	0.95	0.83	0.73
Mount Cook	0.49	0.25	0.99	0.93	0.91	0.70
Picos de Europa	0.59	0.45	1.00	0.99	0.94	0.88
Rocky Mountain	0.49	0.51	0.97	0.99	0.93	0.91
Sierra Nevada	0.61	0.40	1.00	1.00	0.96	0.81
Teide	0.74	0.62	0.98	0.91	0.94	0.78

robustness and network asymmetry was found (Table A1). Difference between plant and pollinator robustness increased with network asymmetry for the three sequences (Fig. 1 and Table A1).

ROLE OF ENDEMIC AND NONENDEMIC PLANTS IN THE CASE-STUDY POLLINATION NETWORKS

Both case-study networks had a significantly modular structure, with four modules in the Picos de Europa network (Modularity = 0.280, $p < 0.01$) and five in the Sierra Nevada network (Modularity = 0.288; $p < 0.01$) (Fig. A2). In the Picos de Europa network, 68% of nonendemic plant species were peripheral, while this percentage rose to 86% for endemic plant species (Fig. 2). In the Sierra Nevada network, endemic species were the only network hubs and there was a higher frequency of nonendemic species having a peripheral role (Figs. 2 and A2). Nevertheless, differences in the frequency distribution of endemic and nonendemic plant species across roles were not significant (Picos de Europa: $p = 0.395$, Sierra Nevada: $p = 0.227$; Freeman-Halton extension of the Fisher exact test).

ROBUSTNESS OF ENDEMIC VS. NONENDEMIC PLANTS TO POLLINATOR EXTINCTION

For the most-to-least linked simulated extinction sequence, the two-way GLM showed a significant effect of both Site and Endemism on robustness to pollinator extinction (Fig. 3). For the random simulated extinction sequence, the two-way GLM showed a significant effect of Site but not from Endemism (Fig. 3). Nevertheless, the interaction between Endemism and Site was significant (Fig. 3). In both simulated extinction sequences, endemic plants were significantly more robust in Sierra Nevada and significantly less robust in Picos de Europa, compared to nonendemic plants (Fig. 3). Under the least-to-most linked simulated extinction sequence, robustness to pollinator extinction of both endemic and nonendemic plants was 1 in both sites.

Discussion

ROBUSTNESS TO PLANT OR POLLINATOR EXTINCTION AND ITS RELATION TO NETWORK PROPERTIES

Previous robustness evaluations (Memmott et al., 2004; Burgos et al., 2007; Kaiser-Bunbury et al., 2010) have found that network robustness is dependent on the species extinction sequence. Namely, it decreases in the order least-to-most linked > random > most-to-least linked. In addition, robustness of pollination networks is considered to be high (Memmott et al., 2004). Our analysis of two Spanish alpine networks and their comparison with a set of 10 additional ASP networks confirmed the robustness order of the extinction sequences. However, it also revealed a broad range of robustness (from $R_{50} = 0.20$ to $R_{50} = 1.00$), rather than a consistently high robustness, particularly for the most-to-least linked sequence. Our results indicated a moderate to high robustness to pollinator extinction and a low robustness to plant extinction (Table 2 and Fig. A1).

A number of reasons can account for the broad range of robustness in the studied ASP networks. Previous empirical and theoretical studies indicate that some structural features influence network robustness. For example, robustness in the least-to-most linked sequence increases when nestedness increases (Burgos et al., 2007); robustness in the random sequence decreases when generalist interactions are more frequent (Pocock et al., 2012); and robustness in all three extinctions sequences increases

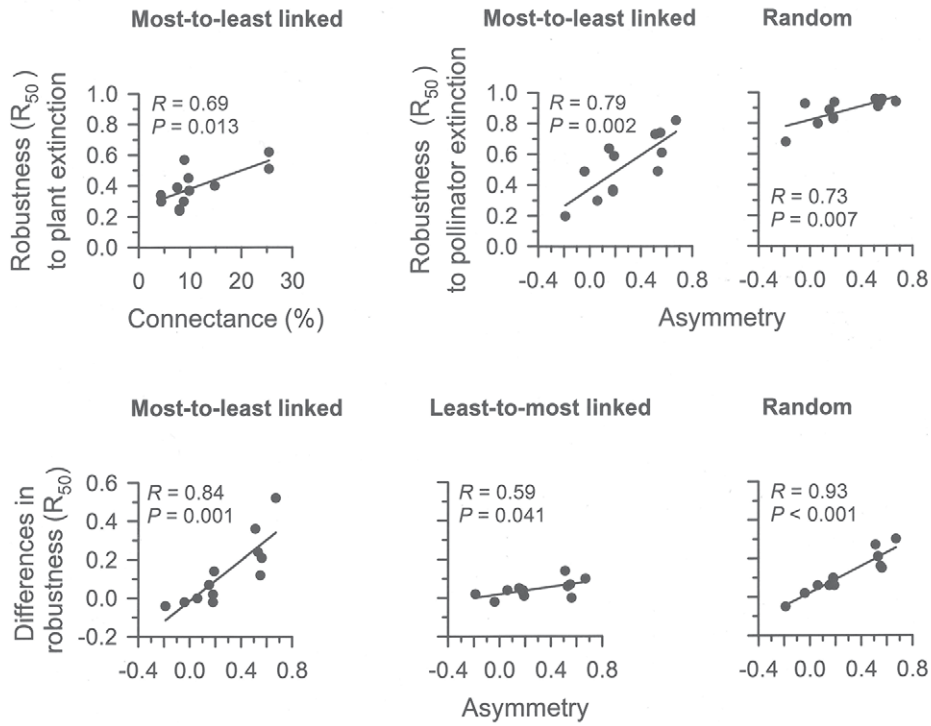

FIGURE 1. Significant Pearson's correlations between network connectance or asymmetry and robustness (measured as R_{50}) to plant or pollinator extinction (upper panels) or to the difference between the robustness to plant and pollinator extinction ("differences in robustness," lower panels). Pearson's correlation coefficient (R) and significance (*P*) are shown. Most-to-least linked:extinction starts in the most connected species; least-to-most linked:extinction starts in the least connected species; random:extinction of species at random.

when primary extinction involves the most species-rich group and when network connectance increases (Pastor et al., 2012). Nevertheless, part of the variability in network robustness in our data set could be due to different sampling quality. Insufficient sampling can overlook pollinators and/or interactions, yielding biased perceptions of network asymmetry and connectance, respectively. Some evidences suggest that pollination networks are undersampled (Chacoff et al., 2012), and the implications of this undersampling for a proper perception of network structure are being increasingly explored. In particular, number of pollinators, number of interactions, interaction frequency and centrality, that is, average relative importance (in terms of connections) of nodes within a network, have been shown to be strongly affected by undersampling (Hegland et al., 2010; Chacoff et al., 2012; Rivera-Hutinel et al., 2012). On the contrary, connectance, modularity, nestedness, and number of plants are weakly affected. A recent key finding (Popic et al., 2013) shows that sampling interactions by means of pollen transported on the pollinator body instead of directly recording visits to flowers can strongly change network structural properties. Nevertheless, network undersampling seems to have limited effects on robustness assessments (Rivera-Hutinel et al., 2012).

In general, our findings for ASP networks agreed with Pastor et al.'s (2012) predictions based on simulated networks: robustness to pollinator (plant) extinction increases (decreases) with increases in asymmetry, and robustness to both plant and pollinator extinction increases with increases in connectance. Previous findings indicate that asymmetry determines the relative robustness to pollinator, compared to plant, extinction by influencing the redundancy of pollinators (Memmott et al., 2004; Ramos-Jiliberto et al., 2012). Robustness ranking of both alpine Spanish networks compared to available ASP networks (Table 2 and Fig. A1) matched their values of connectance and asymmetry. Both networks had intermediate (and similar) connectance in relation with the set of reference ASP networks. However, Sierra Nevada network was the second most asymmetric network, while the Picos de Europa network was relatively symmetric. Accordingly, Sierra Nevada network showed high robustness to pollinator extinction and relatively low robustness to plant extinction, while Picos de Europa network showed relatively high robustness to both pollinator and plant extinction (Table 2 and Fig. A1).

Whether ASP networks are more or less robust than pollination networks in other habitats remains to be studied. Nevertheless, some hints can be obtained from the suggested changes in pollination network structural properties with elevation (Ramos-Jiliberto et al., 2010; Trøjelsgaard and Olesen, 2013). Increases in elevation involve a decrease in pollinator/plant ratio (Ramos-Jiliberto et al., 2010; Trøjelsgaard and Olesen, 2013) and nestedness (Ramos-Jiliberto et al., 2010) and an increase in the number of links per pollinator (Trøjelsgaard and Olesen, 2013). Nestedness increases robustness to the extinction of the least linked species (Burgos et al., 2007) and partner redundancy increases robustness to the three extinction sequences (Pastor et al., 2012) (Fig. 1). This tentatively suggests that increasing elevation could involve: (1) a decrease in robustness under the least-to-most linked sequence due to a decrease in nestedness and (2) a decrease (increase) in robustness to pollinator (plant) extinction due to a decrease in pollinators/plants ratio. At the moment, how these opposing trends combine to produce general patterns of robustness along altitudinal gradients is unknown, but it should be the focus of future research.

NETWORK ROLES AND ROBUSTNESS OF ENDEMIC VERSUS NONENDEMIC PLANTS TO POLLINATOR EXTINCTION

This study provides one of the few empirical results that link, albeit indirectly, robustness with the role of plants in a network. While in Picos de Europa, most endemic plants had few interactions; in Sierra Nevada they were the most linked species,

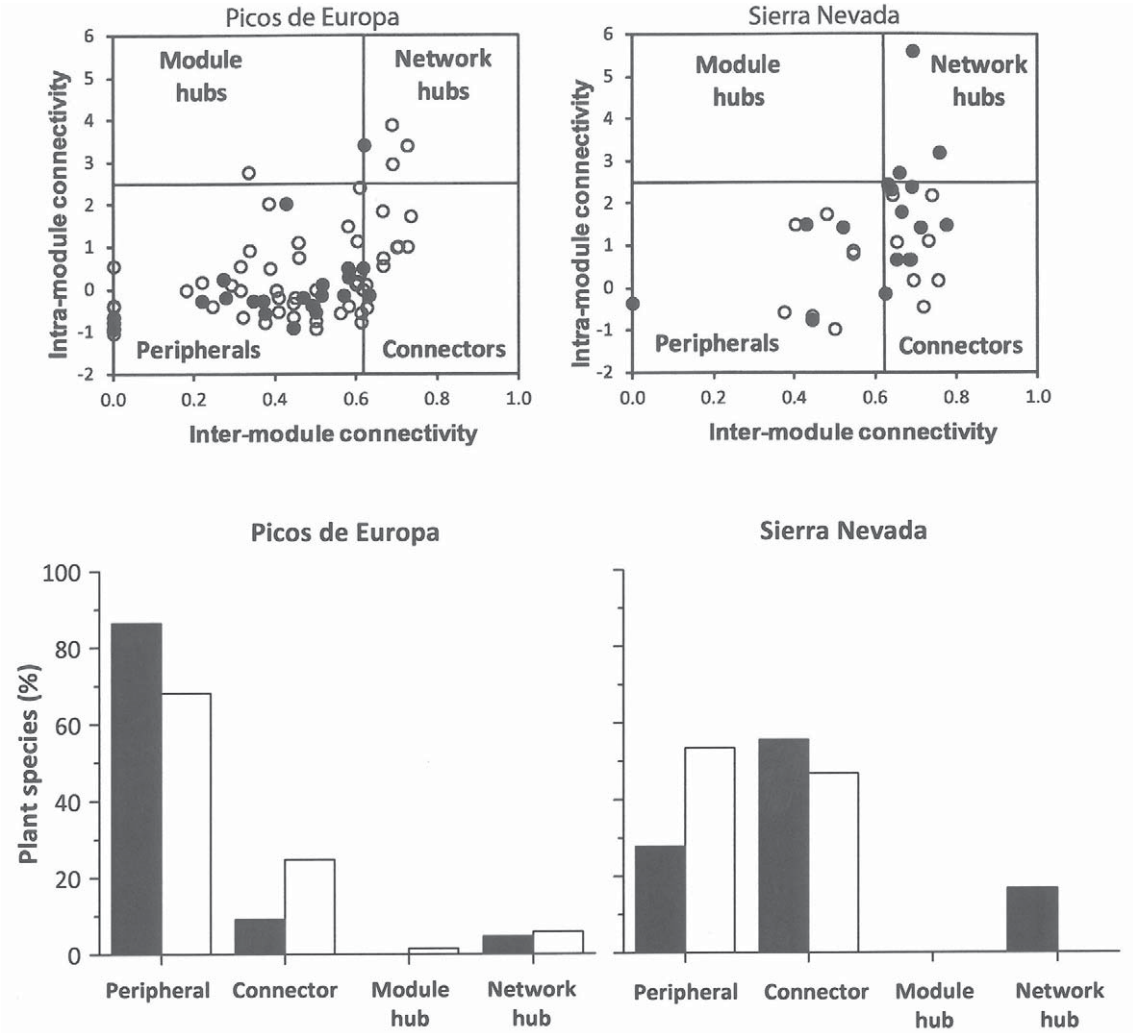

FIGURE 2. (upper panel) Role of endemic (black) and nonendemic (white) plants in each network based on a modularity analysis. Each dot represents a plant species. For clarity, dots for pollinators are not represented. (lower panel) Percentage of peripherals, connectors, module hubs, and network hubs among endemic (black) and nonendemic (white) plant species in each study area.

being essential in holding the network together. Because of their greater number of interactions, plants with a hub role may be more tolerant to random extinction of pollinators and to the extinction of the most connected pollinators than plants with a peripheral or connector role. Our results suggest that in case of extinction of pollinators randomly or beginning by the most connected one (e.g., due to habitat fragmentation) (Pauw, 2007), endemic plants would be significantly more robust than nonendemic plants in Sierra Nevada and significantly more vulnerable in Picos de Europa.

The differences between both Spanish networks in the role and robustness of endemic vs. nonendemic plants underlie the idiosyncratic nature of vulnerability to pollinator extinction. In our two case-study networks, differences could be partially explained by differences in the abundance of the endemic species across networks, because species abundance is a good predictor of the interaction pattern of each plant species (Stang et al., 2006). The most abundant plants could be the most linked ones and, therefore, the most robust to pollinator extinction. In fact, many endemic plants were abundant in Sierra Nevada, while the opposite was true for Picos de Europa. Nevertheless, factors aside from abundance have been recently identified as important for the number of interactions in pollination networks, such as temporal or morphological match or mismatch between pollinators and plants (Vizentin-Bugoni et al., 2014). Features of particular plant species and community assemblage history, responsible for differences in network role or vulnerability to pollinator extinction, deserve future attention.

POLLINATION NETWORK ROBUSTNESS AS A CONSERVATION TOOL: A LIST OF CAVEATS

With pollination interactions facing increasing threats, tools for early detection of risks such as assessment of robustness of pollination networks offer great promise. Thus, it is important to be aware of several caveats in order to properly assess the utility of this approach. In the following, we focus on three important aspects (Fig. 4): the order in which species of the network will get extinct (network disassembly), the way to incorporate the possibility of rewiring once a species has lost all of its partners (rewiring rules), and the importance of each pollination interaction for species persistence (interaction importance).

First, empirical evidence about the way pollination networks disassemble is needed to ascertain which of the suggested

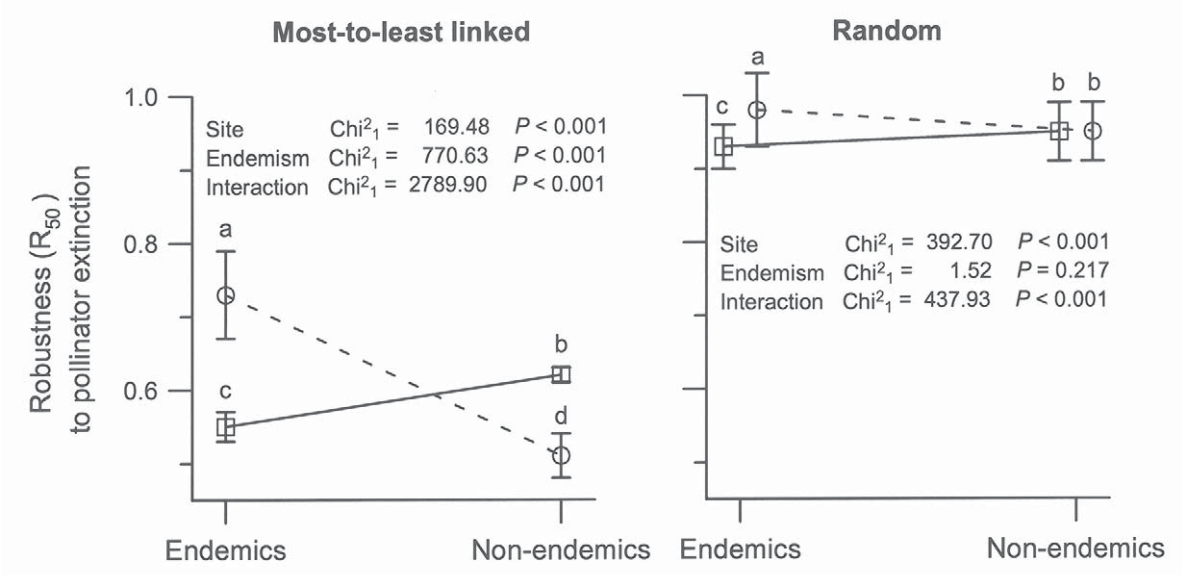

FIGURE 3. Mean robustness (R_{50}) to pollinator extinction of endemic and nonendemic plants under the most-to-least linked (left) and random (right) sequences of pollinator extinction for Picos de Europa (continuous line and squares) and Sierra Nevada (dashed lines and circles). *N* = 300 in all cases. Error bars correspond to standard deviation. Chi-squared (Chi^2) and significance (*P*) of a two-way general linear model (GLM) comparing differences in robustness between site and endemism factors are shown. Average values with different letters were significantly different according to an a posteriori Tukey honest significant differences test. For clarity, symbols in the right panel have been slightly moved to avoid overlap.

extinction sequences is more likely to occur. Evidence suggests nonrandom order of species extinction (Saavedra et al., 2011). In addition, alternative extinction scenarios should be considered. For example, link (as opposed to node) extinction has been suggested (Pastor et al., 2012), and its differences in robustness with respect to node extinction are being assessed (S. Santamaría et al., unpublished data). In the absence of empirical evidence about how pollination networks disassemble in response to species extinction, useful information can be obtained by studying the opposite process, that is, network assembly (Pocock et al., 2012). Studies of pollination network assembly in successional ecosystems, such as gradients of deglaciation, offer good starting points (Albertch et al., 2010). Another possibility could be to explore likely scenarios of extinctions for alpine environments. For example, we could

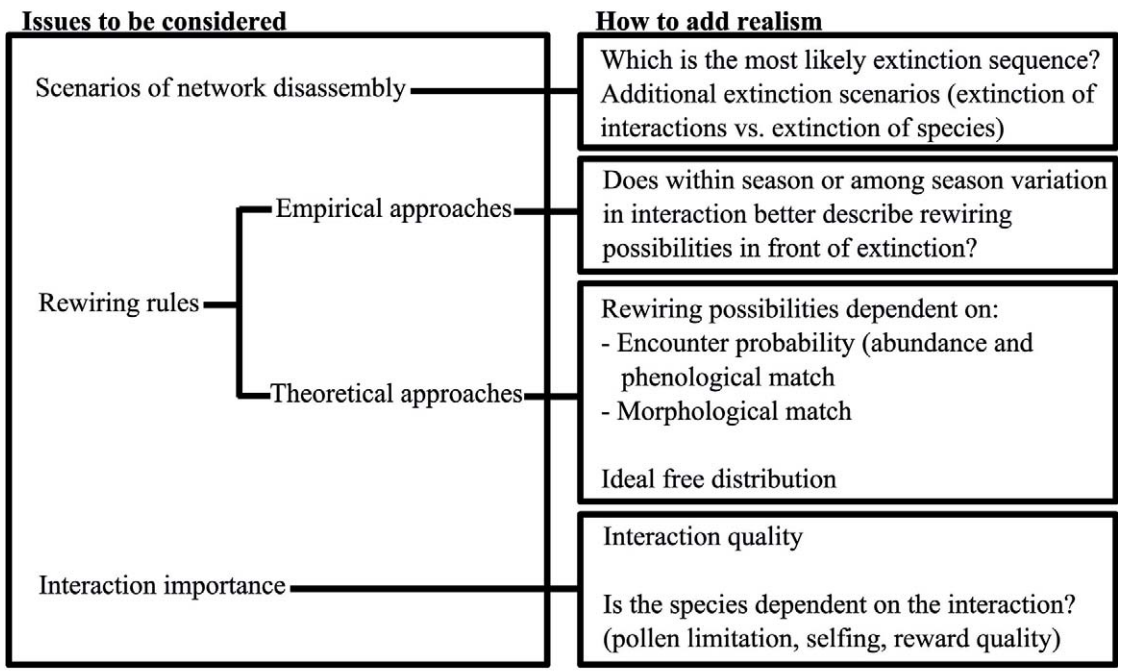

FIGURE 4. A list of caveats to be addressed to improve the realism of robustness assessing methods based on the simulation of extinction of mutualistic partners.

simulate species extinction sequences driven by climate warming assuming that mountain-specialist species become extinct first, or driven by encroachment, by simulating an increasing abundance of shrubby species in detriment of herbaceous ones.

Second, the possibility of rewiring should be incorporated into the robustness assessment (Staniczenko et al., 2010; Kaiser-Bunbury et al., 2010; Benadi et al., 2012; Ramos-Jiliberto et al., 2012). After losing all its partners, a species does not necessarily become extinct, but it can reconnect (rewire) to other species. We can distinguish two approaches to define rewiring rules: empirical and theoretical. Empirical approaches to rewiring have relied either on within-season phenological changes in interactions (Olesen et al., 2008; Kaiser-Bunbury et al., 2010; Ollerton et al., unpublished data) or on between-season variation in interactions (Petanidou et al., 2008). We consider the latter as more informative, but comparisons among them are needed. In contrast to these empirical models, other studies (Staniczenko et al., 2010; Benadi et al., 2012) apply theoretical models such as those based on niche theory. The underlying logic is that rewiring occurs as a result of niche release caused by species extinction. Modeling rewiring rules involves detailed studies of competition interactions between pollinators and foraging behavior (Ohashi, 2002; Ishihama and Washitani, 2007; Rodríguez-Gironés and Santamaría, 2010) and the probability of plant-pollinator encounter (including abundance and phenology) and morphological adjustment (Santamaría and Rodríguez-Gironés, 2007; Stang et al., 2009). We suggest that the ideal free distribution models (Fretwell and Lucas, 1970; Dreisig, 1995) could provide useful insights on rewiring possibilities in pollination networks.

Third, in order to evaluate the impact of interaction loss, we must consider that not all interactions are equally important. Current evidence is mixed. Recent research in a network suggests that interaction frequency is a good surrogate of interaction strength (Vázquez et al., 2012), although evidence also exists for a role of pollinator quality (Rodríguez-Gironés and Santamaría, 2010; King et al., 2013). Fitness dependence requires detailed information about, among others, the plant capacity for self-pollination and clonal propagation, the pollinator effectiveness, and the benefit for the pollinator of plant rewards. For example, determining self-compatibility and pollen limitation degree of plants would more realistically evaluate their dependence on pollinators (Schoen and Lloyd, 1992; Knight et al., 2005). In alpine environments it is particularly relevant to know the interaction importance because (1) they are ecosystems in which pollen limitation is frequent (García-Camacho and Totland, 2009), (2) changes in character stages resulting from adaptation to alpine conditions in endemic alpine plants make it difficult to predict their selfing capacity based on available information about their congeners, and (3) pollination effectiveness of dominant visitors, such as flies, in many mountains has been little studied.

Conclusions

Alpine pollination networks showed a broad range in robustness, partially due to differences in network asymmetry. In addition, our results about the network role and robustness of endemic plant species to pollinator extinction suggested that the vulnerability of endemic plants depends on particularities of each pollination network, such as abundance and floral morphology of endemic and nonendemic plants. To improve the utility of robustness assessment for conservation purposes, we have identified three caveats requiring attention—namely, knowledge about the sequence of network disassembly, the rewiring rules, and how fitness depends on the interaction. Efforts along these three lines of work will provide more realistic predictions of pollination network response to the disassembly of their interactions.

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APPENDIX

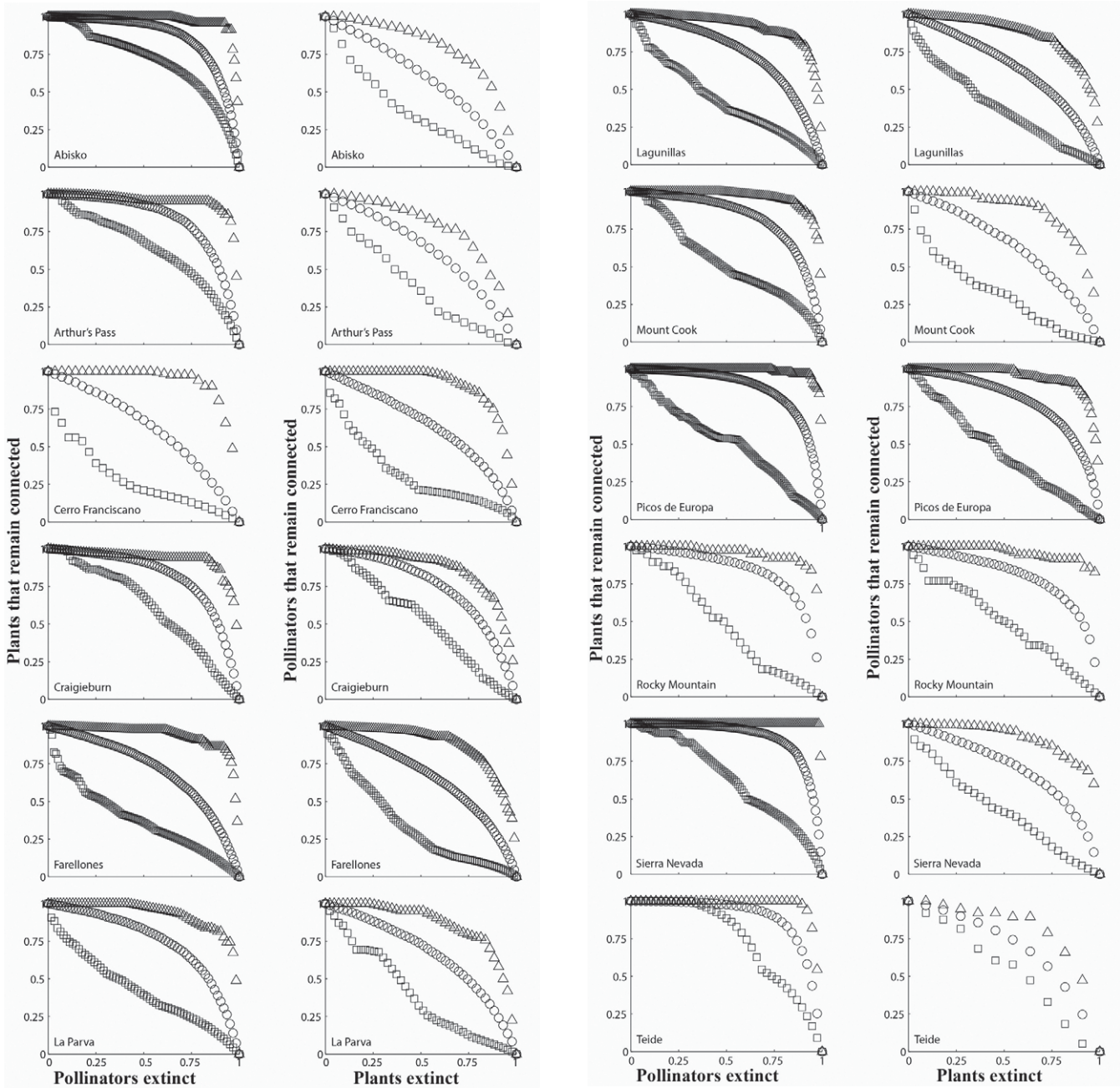
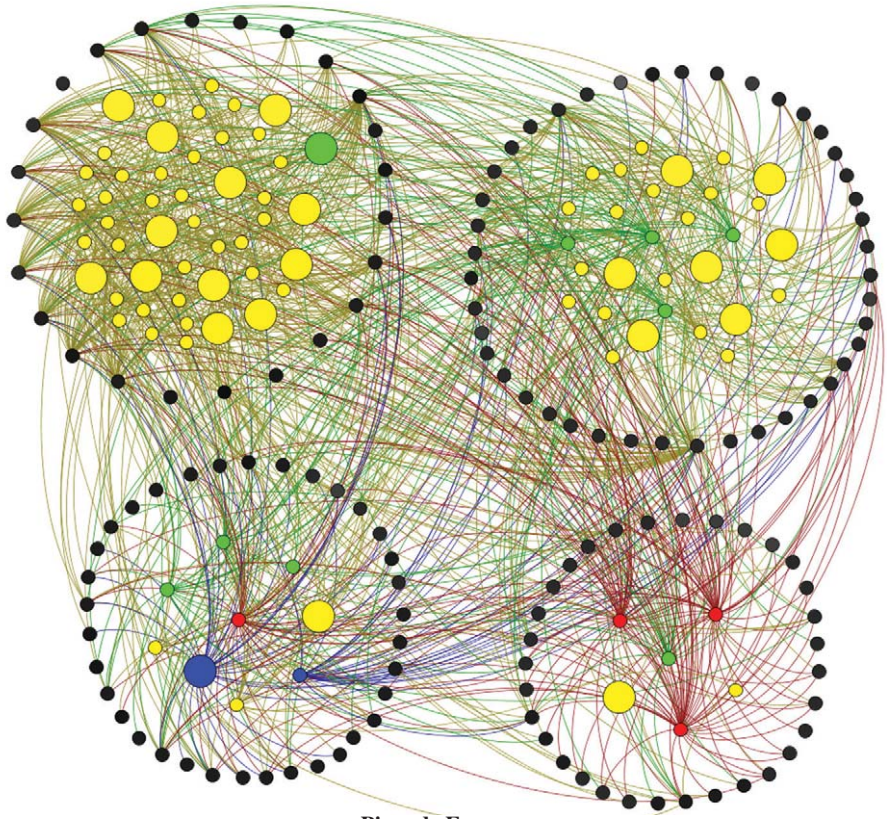
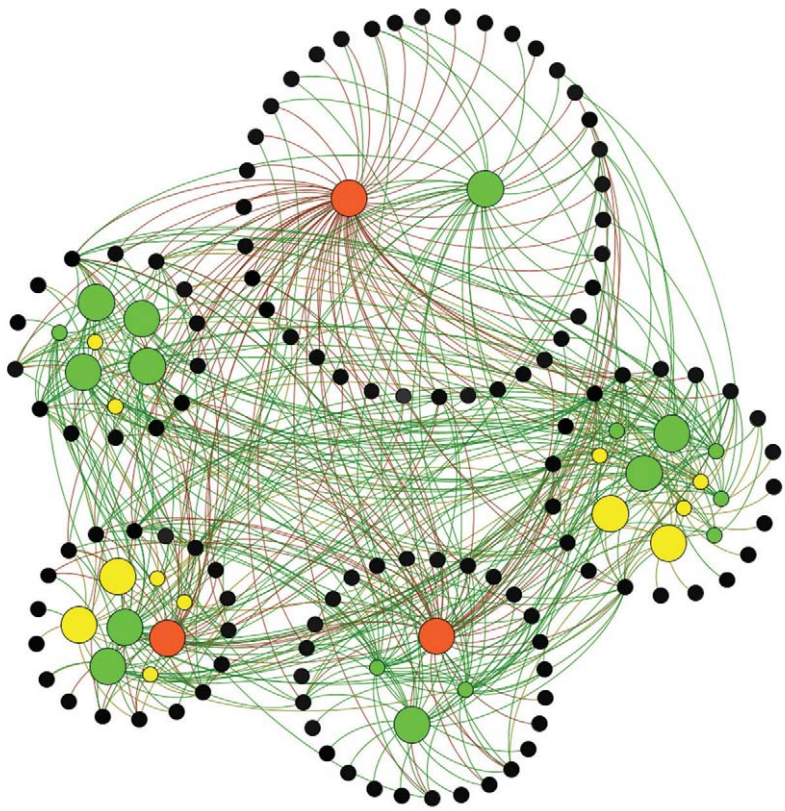


FIGURE A1. Extinction curves showing the proportion of plant (left) and pollinator (right) species which remain in the network as a function of the proportion of species in the opposite taxon (pollinators and plants, respectively) that go extinct. The symbols indicate the extinction sequence: squares, primary extinction beginning by the most-linked species; triangles, primary extinction beginning by the least-linked species; circles, random extinction.



Picos de Europa



Sierra Nevada

FIGURE A2. Picos de Europa and Sierra Nevada network modular structure. Each circle represents a species (pollinators in black), and each line represents an interaction between a plant and a pollinator species. Species were grouped according to the module to which they belong. Colors indicate the plant role for network cohesion: red, network hub; green, connector; blue, module hub; yellow, peripheral. Large circles indicate endemic plants.

Table A1

Pearson's correlation coefficient (*R*) and significance (*P*) of the relationship between network connectance or asymmetry and robustness to plant extinction, robustness to pollinator extinction, or the difference between robustness to plant and pollinator extinction. Three sequences of primary species extinction were simulated: most-to-least linked (extinction starts in the most connected species); least-to-most linked (extinction starts in the least connected species); and random (extinction of species at random).

		Connectance		Asymmetry	
		R	*P*	*R*	*P*
Most-to-least linked	Robustness to pollinator extinction	0.392	0.208	0.786	0.002
	Robustness to plant extinction	0.692	0.013	0.050	0.879
	Differences between robustness to plant and pollinator extinction	—	—	0.841	0.001
Least-to-most linked	Robustness to pollinator extinction	–0.348	0.267	0.535	0.073
	Robustness to plant extinction	0.144	0.655	–0.484	0.111
	Differences between robustness to plant and pollinator extinction	—	—	0.595	0.041
Random	Robustness to pollinator extinction	0.467	0.126	0.731	0.007
	Robustness to plant extinction	0.529	0.077	–0.431	0.162
	Differences between robustness to plant and pollinator extinction	—	—	0.929	<0.001