Plant interactions shape pollination networks via nonadditive effects

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Abstract. Plants grow in communities where they interact with other plants and with other living organisms such as pollinators. On the one hand, studies of plant–plant interactions rarely consider how plants interact with other trophic levels such as pollinators. On the other, studies of plant–animal interactions rarely deal with interactions within trophic levels such as plant–plant competition and facilitation. Thus, to what degree plant interactions affect biodiversity and ecological networks across trophic levels is poorly understood. We manipulated plant communities driven by foundation species facilitation and sampled plant–pollinator networks at fine spatial scale in a field experiment in Sierra Nevada, Spain. We found that plant–plant facilitation shaped pollinator diversity and structured pollination networks. Nonadditive effects of plant interactions on pollinator diversity and interaction diversity were synergistic in one foundation species networks while they were additive in another foundation species. Nonadditive effects of plant interactions were due to rewiring of pollination interactions. In addition, plant facilitation had negative effects on the structure of pollination networks likely due to increase in plant competition for pollination. Our results empirically demonstrate how different network types are coupled, revealing pervasive consequences of interaction chains in diverse communities.

Key words: biodiversity; competition; ecological networks; ecosystem functioning; facilitation; foundation species; interaction chains; interaction diversity; nestedness; pollination.

INTRODUCTION

Plants grow in communities where they interact with other plants (Tilman 1994, Callaway et al. 2002, Levine et al. 2017, Mayfield and Stouffer 2017) and with other organisms such as pollinators (Bascompte et al. 2003, Bastolla et al. 2009, Bronstein 2009). The consequences of plant interactions are fundamental for plant community diversity (Bruno et al. 2003, Cavieres et al. 2014, Kikvidze et al. 2015) and stability (Levine et al. 2017, Losapio and Schöb 2017, Mayfield and Stouffer 2017). A growing literature examines the effects of competition and facilitation among plants for the structure of insect communities (Ghazoul 2006, Valiente-Banuet and Verdú 2013). In particular, there is evidence that plants can

facilitate the pollination of their neighboring plants by increasing overall neighborhood attractiveness (Sieber et al. 2011, Reid and Lortie 2012, Mesgaran et al. 2017). Yet studies of plant–plant interactions do not consider networks of interactions among plants and with other trophic levels such as pollinators. Whereas studies of plant–animal interactions do not deal with direct interactions within trophic levels such as plant–plant competition and facilitation. Despite wide-ranging implications for ecosystem functioning and services (Hector et al. 1999, Schöb et al. 2015), fundamental questions remain about how interactions between plants scale up to plant–pollinator interactions and ultimately shape pollination networks. Addressing these questions is urgent as pollination is a fundamental ecosystem service (Potts et al. 2016) that may depend on effects of plant interactions.

The structure of pollination interactions is usually analyzed by means of bipartite networks (Bascompte et al. 2003, Olesen et al. 2007, Bastolla et al. 2009, Dormann et al. 2009). In this framework, plant and pollinator species represent the two sets of the network and pollinator visits represent interactions between them. Nevertheless, direct interactions within trophic levels such as competition or facilitation between plants are not considered in bipartite networks. Indirect interactions in plant communities deal with the fact that interactions between two plant species may change in the presence of a third plant species (Levine 1999, Levine et al. 2017, Mayfield and Stouffer 2017). Analogously, we expect that the presence of a plant may alter the interactions between another plant and its pollinators (Feldman et al. 2004, Ghazoul 2006, Sieber et al. 2011, Mesgaran et al. 2017). For instance, foundation species, i.e., plant species that modify environmental conditions with disproportionately large effects on other plants (Ellison et al. 2005), may affect the pollination of associated plants by affecting pollinator behavior and

changing the overall attractiveness of the community (Fig. 1). Such indirect interactions may in turn affect the structure and robustness of ecological networks (Sauve et al. 2014, Levine et al. 2017). However, there is a gap of knowledge about how direct effects of interactions within trophic levels influence interaction networks between trophic levels (Fig. 1a). Particularly, we do not know to what extent chains of plant–plant–pollinator interactions affect biodiversity and shape pollination networks (Fig. 1b). We operatively consider interaction chains as the set of direct species interactions in which the presence of species at a given trophic level affects patterns of interactions at a different level. For instance, plant A affects pollination interactions of plant B by directly facilitating (e.g., via reducing soil disturbance or increasing floral rewards) or inhibiting it (e.g., via limiting flower accessibility to pollinators). Coupling several interaction networks may shed light on the organization of biodiversity. In addition, knowledge about interaction chains in natural communities can help in developing informed decision-making for managing ecosystem services.

In this study, we investigated the effects of plant–plant–pollinator interactions on biodiversity and pollination networks (Fig. 1b). We hypothesized that plant facilitation for growth and survival influences pollination networks via nonadditive effects through increasing pollinator attraction. We expected that pollination networks in facilitation-driven communities are more diverse and nested than the combination of their parts. To test our hypothesis, we built networks by combining pollination interactions of foundation and associated plant species growing separately to obtain a single network (hereafter referred to as "additive" network). These additive networks were then compared with the observed pollination networks of the community where foundation and associated plant species grew together (hereafter referred to as "control" networks; Fig. 1b). Our
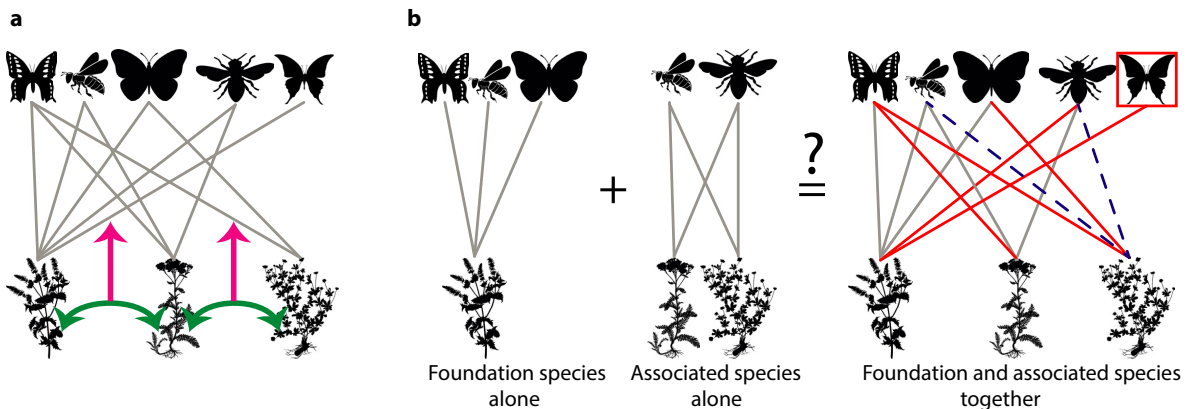

FIG. 1. Ecological networks including interaction chains between plants and pollinators. (a) Direct interactions between plants (green arrows) can affect (magenta arrows) plant–pollinator interactions (gray links). (b) Pollination interactions and biodiversity are nonadditive, i.e., do not hold the same if species grew together or not. Indeed, pollination interactions may occur only in the presence (red links) or absence (dashed blue links) of other plant species, thus affecting biodiversity and pollination networks (see additional species in the red square).

study empirically demonstrates how interactions between plants and pollinators change in the presence of other plant species, highlighting the consequences of plant–plant interactions for pollinator diversity and the structure of pollination networks.

MATERIAL AND METHODS

Experimental setting

We conducted a field-removal experiment with two foundation plant species (*Arenaria tetraquetra* ssp. *amabilis* and *Hormathophylla spinosa*) and eight associated plant species (Appendix S1: Fig. S1) in an alpine plant community from the Sierra Nevada Mountains, Spain (Loma del Mulhacén, 3200 m above sea level; 37.041417° N, 3.306400° W; Appendix S1: Fig. S2). In this well-established model ecosystem, beneficial and harmful effects of plant facilitation have been studied for several years (Callaway et al. 2002, Schöb et al. 2012, 2014, Cavieres et al. 2014, Kikvidze et al. 2015, Losapio and Schöb 2017). These two foundation species enable plant coexistence providing positive facilitative effects on other associated plant species through the improvement of their physiological status (Schöb et al. 2012, 2013). Mechanisms are due to the decrease of stress followed by the increase of soil water content and organic matter in foundation-species communities compared to bare ground. Conversely, associated plant species have harmful effects on foundation species, decreasing their flower and seed production (Schöb et al. 2014).

We assembled three types of plant communities representing the facilitation system and its parts: (1) foundation plant species blooming alone, (2) associated plant species blooming alone, and (3) foundation and associated species blooming together (Fig. 1b). We considered the naturally occurring plant communities with foundation species and associated species blooming together as positive control. In the removal treatments, we either covered foundation species (to have associated species blooming alone) or clipped associated species (to have foundation species blooming alone). We followed a randomized block design, where each block was composed by the two removal treatments of foundation species and associated species blooming separately and the control of foundation species and beneficiary species blooming together (Fig. 1). Each block consisted of three plots of 20 × 20 cm standard size. This fine spatial scale is the same scale at which plant–plant facilitation is working (Schöb et al. 2012), it is the typical patch size and it is consistent with the small stature of alpine plants as well as with pollinator foraging (Chittka and Thomson 2001). Distance among plots within a block ranged between 0.5 m and 1 m as is sufficient for having isolated microhabitats given the patchy vegetation structure. Even though pollinators might move over longer distance, floral choice is evaluated at the centimeter scale

(Harden and Waddington 1981, Chittka and Thomson 2001). Thus, with our experimental setup we looked at plant neighborhood effects on choices by foraging insects from a single species pool rather differences among species pools. In total, 14 blocks replicated over each foundation species community were randomly established at least 10 m apart within a relatively homogeneous area of about 1 ha, resulting in 84 plots in total. Plant species diversity did not vary between foundation species ($P = 0.114$), treatments ($P = 0.832$), or both ($P = 0.649$). Plant species composition was similar across blocks and treatments (Appendix S1: Fig. S3). Among-block differences were accounted for in statistical analyses as random effects.

Pollinator visits to plants were observed during the entire flowering season of July 2015. We defined pollination interactions as the contact between pollinators and sexual reproductive parts of plant flowers. Thanks to an exceptionally dry spring and a warm summer, plants completed their flowering phase within three weeks during July. Hence, we were able to cover the complete flowering time for most of the species at our study site. Each plot was sampled during a standardized time span of 20 minutes a day. The three plots belonging to the same block were sampled together, in order to eliminate within block variability due to sampling weather conditions. Every day, 14 sampling rounds were carried out between 10:00 and 17:30 (blocks randomly sampled). Each block was sampled between six and nine times, resulting in 204 sampling rounds in total (Appendix S1: Table S2). The pollinators of each flower (plant species) in each plot were recorded and sampled using a sweep net and an entomological aspirator. Due to conservation issues related to Sierra Nevada National Park legislation and also sampling and ethical issues, we limited the collection of bees, bumblebees, hoverflies, and butterflies to those necessary for species identification. These groups represented 88% of pollinator fauna (Appendix S1: Fig. S4). Insects were identified at the species level whenever possible, otherwise to genus or family. As not all the flower-visiting insects are actual pollinators, we excluded from the analysis all the non-pollinator species on the basis of expert knowledge (Appendix S1: Table S3). Insect specimens are stored at the ETH insect collection and in our institutions.

Network analysis

To quantify nonadditive effects arising from plant facilitation, we compared "control" networks with "additive" networks. The control network was constructed from the data collected on the intact plant community (positive control treatment). We built additive networks by pooling plant and pollinator species and their interactions in the two treatments of foundation and associated species growing alone. We highlight that this type of comparison is a more conservative approach than considering the mean of the two component treatments because the

additive network was sampled twice as much as the control network. Therefore, additive networks may have higher insect abundance and diversity because they result from the pool of two plots rather than from one plot as control networks. However, we believe that our approach is not only more conservative but also more accurate because we keep the diversity of plants and flowers similar between additive and control networks and we further standardized metrics for sampling effort.

Pollinator diversity was calculated as Shannon diversity of pollinators per flower diversity per sampling hour. It was calculated at the plot level ($n = 84$). Pollinator visitation rate was calculated as pollinator abundance divided by the number of flowers and sampling hours (log-scaled). It was calculated at the plot level for each plant species associated with each foundation species (Appendix S1: Fig. S5). This way we accounted for the response of pollinator abundance to flower density (Losapio et al. 2016).

Network structure was calculated according to the measure of nestedness η (Bastolla et al. 2009). Nestedness was calculated for pooled additive and control networks, i.e., pooling data across blocks for each foundation species ($n = 4$). We chose this metric instead of the more commonly applied NODF because the latter does not take into account contribution to nestedness of pairs of species having the same number of interactions (i.e., species degree; Appendix S1: Table S6). In our case, given the long tail of pollinator abundance distributions, it is important to consider to what extent pollinators that visited only one or a few plant species share their partners regardless of their degree. This nestedness was therefore calculated with an improved measure, $\eta = \frac{1}{2} \left(\sum_{i<j} \frac{n_{ij}^{pl}}{\min\left(n_i^{pl}, n_j^{pl}\right)} + \sum_{i<j} \frac{n_{ij}^{pol}}{\min\left(n_i^{pol}, n_j^{pol}\right)} \right)$ where n_{ij} is the number of interactions n between two plant (pl) or two pollinator (pol) species i and j and $\min(n_i, n_j)$ is the smaller of the two values.

To estimate the significance of each observed network nestedness, we compared the empirical nestedness η with the distribution of 999 random networks. Random networks were built according to a probabilistic null model (Bascompte et al. 2003). This null model has been found to have a good performance in the context of the trade-off between type I and type II errors (Rodríguez-Gironés and Santamaría 2006), and it is most biologically meaningful in terms of species generalization (i.e., node degree). This randomization builds networks from a template of interaction probabilities, such that in an adjacency matrix $\mathbf{A} = \mathbf{R} \times \mathbf{C}$ with $\mathbf{R}$ rows and $\mathbf{C}$ and columns, the probability that a cell a_{ij} has a link is $\frac{1}{2}\left(\frac{a_i}{C} + \frac{a_j}{R}\right)$, where a_i and a_j is the number of links in column and row, respectively. Only random networks with $\mathbf{R}$ and $\mathbf{C}$ equal to empirical networks were retained.

A direct comparison of nestedness between additive and control networks is not possible because of different matrix sizes. To compare nestedness between "facilitation" and additive networks, we calculated the relative nestedness using the Z score principle. We calculated the deviance of the empirical nestedness from random expectation given by the 999 replicates of probabilistic networks as $Z = \frac{o - \bar{r}}{sd(r)}$ where o is the empirical value, $\bar{r}$ the mean value across network randomization, and $sd(r)$ the standard deviations across randomizations.

Finally, we examined potential mechanisms that might explain nonadditive effects and their consequences for network structure. We tested for differences in species interactions beyond differences in species composition and richness. We compared additive and control networks ($n = 4$) composed only of those shared pollinator species (Fig. 2). We first quantified the network dissimilarity between shared-species additive and facilitation networks using the beta diversity of interactions (Poisot et al. 2012). We then calculated the species-level diversity of interactions in these shared-species networks using the Shannon index (Oksanen et al. 2017). Overall, the analyzed metrics are only weakly correlated and therefore show limited bias (Fründ et al. 2016).
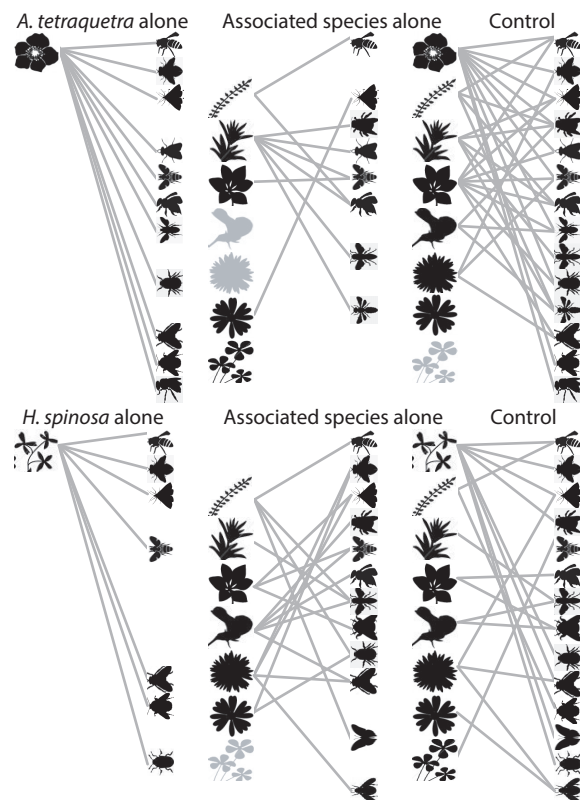

FIG. 2. Pollination networks of the three experimental treatments. We built additive networks by pooling data of foundation species and associated plants alone treatments. Networks displayed were built with pollinator species shared by additive and control networks. Plants in black and without links were not visited by shared pollinators. Plants in gray were never visited. See Appendix S1: Fig. S1 for species names.

Statistical analysis

To assess changes in pollinator diversity, visitation rate and interaction diversity (responses, three different models), we used linear mixed-effects models. Fixed effects were network type (i.e., additive and control), foundation species identity (i.e., *A. tetraquetra* and *H. spinosa*), and their interaction term. Plant species identity and blocks were random effects. Trophic level (i.e., either plant or pollinator) was a fixed effect too when analyzing interaction diversity. To assess the significance of specific combinations of fixed factors, we used least-squares means contrasts (Lenth 2016). We tested the significance of observed network nestedness as

$$P' = 1 - \sum_i^S I[H_{\text{obs}} > H_j]/s, \text{ where } I[H_{\text{obs}} > H_j] \text{ is an}$$

indicator function that equals 1 if the observed nestedness was greater (or smaller) than the random value and 0 otherwise, across $s = 999$ simulations + 1 empirical value. Data analysis was done in R version 3.3.3 (R Core Team 2017).

RESULTS

Pollinator diversity

We found that pollinator diversity significantly differed between control networks and additive networks
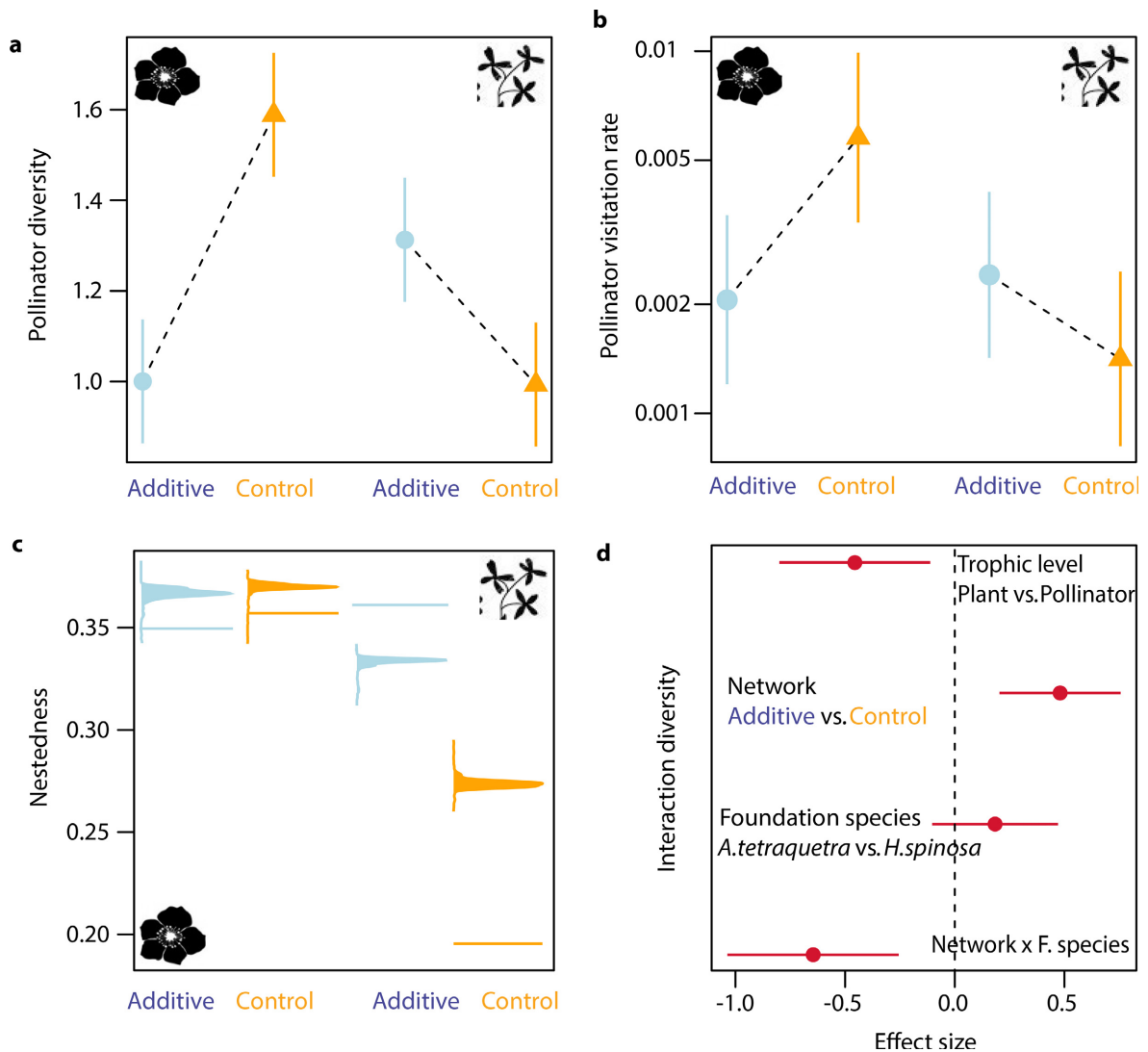

FIG. 3. Effects of plant interactions on pollination networks associated with foundation (F) species *Arenaria tetraquetra* (left) and *Hormathophylla spinosa* (right). (a) Pollinator diversity. Least-square means and 95% CI shown. (b) Pollinator visitation rate. Least-square means and 95% CI shown. (c) The nested structure of plant–pollinator networks. Horizontal bars show the empirical nestedness η. Curves show the distribution of nestedness in probabilistic networks. (d) Response of interaction diversity in shared-species networks to trophic level, networks and foundation species identity. Estimates and 95% CI shown.

TABLE 1. Summary of mixed-effects models testing differences in pollinator diversity, visitation rate, and interaction diversity of plant and pollinator species between additive and control networks and foundation species (*Arenaria tetraquetra* and *Hormathophylla spinosa*).

Response and predictor	Estimate	SE	t	P
Pollinator diversity				
Network	0.59	0.16	3.76	<0.001
Foundation species	0.31	0.16	2.00	0.053
Network × Foundation species	−0.91	0.22	−4.10	<0.001
Pollinator visitation rate				
Network	1.03	0.50	2.05	0.043
Foundation species	0.16	0.55	0.29	0.776
Network × Foundation species	−1.57	0.73	−2.14	0.034
Interaction diversity				
Trophic level	−0.46	0.17	−2.72	0.011
Network	0.48	0.14	3.48	0.001
Foundation species	0.18	0.14	1.28	0.205
Network × Foundation species	−0.65	0.20	−3.13	0.002

Note: Intercepts not shown.

($\beta = 0.59 \pm 0.16$ [mean ± SE], $t = 3.76$, $P < 0.001$) depending on the identity of foundation species ($\beta = -0.91 \pm 0.22$, $t = -4.10$, $P < 0.001$; Fig. 3a, Table 1). In particular, *A. tetraquetra* control networks were ~60% more pollinator-species diverse than additive networks ($q = 0.59 \pm 0.16$, $t = 3.76$, $P = 0.0030$; Appendix S1: Table S4). Differences were not significant for *H. spinosa* ($q = -0.32 \pm 0.16$, $t = 2.04$, $P = 0.1903$). These results suggest that nonadditive effects of plant interactions on pollinator diversity were synergistic in *A. tetraquetra* communities while they were additive in the presence of *H. spinosa*.

Pollinator attraction

Pollinator visitation rate differed between additive and control networks ($\beta = 1.03 \pm 0.50$, $t = 2.05$, $P = 0.043$) depending on the identity of foundation species ($\beta = -1.57 \pm 0.73$, $t = 2.05$, $P = 0.034$; Fig. 3b, Table 1). Despite no significant differences were found for specific contrasts (Appendix S1: Table S4), plants associated with *A. tetraquetra* in control networks were ~100% more attractive than plants in additive networks ($q = 1.03 \pm 0.50$, $t = 2.05$, $P = 0.177$), while plants associated with *H. spinosa* in control networks were ~50% less attractive than plants in additive networks ($q = 0.53 \pm 0.53$, $t = 1.00$, $P = 0.745$). This indicates that plant neighbors affected chances of getting visited by pollinators in different ways between foundation species.

Network structure

Both additive and control networks in *A. tetraquetra* were significantly anti-nested ($Z = -2.11$, $P' = 0.036$; $Z = -5.19$, $P' = 0.008$, respectively; Fig. 3c, Appendix

S1: Table S5). Relative nestedness was more than two times higher in *A. tetraquetra* additive network compared to the control network. Conversely, additive network of *H. spinosa* was significantly nested ($Z = 6.69$, $P' < 0.001$) while control network of *H. spinosa* was significantly anti-nested ($Z = -6.54$, $P' < 0.001$). These results indicated that plant interactions shaped the structure of pollination networks via nonadditive effects in *H. spinosa*.

Species turnover and interaction rewiring

We next disentangled differences between additive and control networks related to changes in species composition, i.e., species turnover, from differences due to interaction rewiring, i.e., the changes in interactions between a given set of plants and pollinators. Network dissimilarity was 42.3% for both foundation species (Appendix S1: Fig. S7). In *A. tetraquetra*, 47.3% of this dissimilarity was due to interaction rewiring and 52.7% due to pollinator turnover. In *H. spinosa*, 59.1% was due to interaction rewiring and 40.9% due to pollinator turnover. These results indicate that additive and control networks were different because they had both different pollinator species composition and because the pollinators they shared show different interactions with the same plant species.

Interaction diversity

Having shown that interaction rewiring contributes to differences between networks, we examined additive and control networks composed only by shared species (Fig. 2). Species-level interaction diversity significantly differed between shared-species additive and control networks ($\beta = 0.48 \pm 0.14$, $t = 3.48$, $P = 0.001$) depending on foundation species ($\beta = -0.46 \pm 0.17$, $t = -2.72$, $P = 0.011$; Fig. 3d, Table 1). Specifically, interaction diversity among shared species was higher in *A. tetraquetra* control network than expected by additive effects ($q = 0.48$, $P = 0.005$; Appendix S1: Table S4) but as much as expected in *H. spinosa* ($q = -0.17$, $P = 0.614$; Appendix S1: Table S4). These results indicate that plant–plant interactions promoted rewiring of pollination interactions, increasing interaction diversity in the case of *A. tetraquetra*.

DISCUSSION

Our findings of nonadditive effects of plant facilitation on pollination networks shed new light on the poorly understood mechanisms underlying biodiversity maintenance across trophic levels. Direct interactions between foundation and associated plant species produced synergistic and antagonistic effects that affected biodiversity and the structure of pollination networks. The sign of these nonadditive effects varied between foundation species. After controlling for differences in pollinator species composition and richness, we found

that plant facilitation rewired pollination interactions increasing interaction diversity. Taken together, our results indicate how different network types are coupled, revealing that removing species can have disproportionate effects on ecological networks.

Similar effects as the ones reported here were found by pioneering studies of Paine (1966). He showed trophic cascades in food webs on rocky shores, where keystone predator species had top-down effects that controlled multiple trophic levels. We found that foundation species mediated pollination networks but with bottom-up rather than top-down control. When removing and isolating the effects of plant species on floral visitors, pollination interactions changed, as did interaction diversity and network structure. Such nonadditive effects were previously reported empirically only in plant communities (Levine et al. 2017, Mayfield and Stouffer 2017) or considering predator–prey interactions (e.g., Paine 1966). Notably, our findings indicated that a species can promote the rewiring of interactions among other species in the community. Such interaction rewiring may be due to the plasticity of pollinator behavior.

Our results support the hypothesis that positive plant–plant interactions may influence plant–pollinator interactions. In the examined communities from the Sierra Nevada in Spain, the foundation plant species *A. tetraquetra* and *H. spinosa* improved the ecophysiological status of associated plants (Schöb et al. 2012, 2013, 2014), increased plant diversity (Cavieres et al. 2014, Kikvidze et al. 2015) and the resistance of the plant communities in response to drought (Losapio and Schöb 2017) while they were harmed by the presence of associated species (Schöb et al. 2014). Moreover, our findings are in accordance with other studies showing the beneficial effects of foundation species on pollinator diversity (Sieber et al. 2011, Reid and Lortie 2012) and the linkages between the structure of plant and insect communities (Ghazoul 2006, Valiente-Banuet and Verdú 2013, Robinson et al. 2018). Besides direct facilitation by foundation species, a potential mechanism can be the cluster effect (Porter 1998). This is a socioeconomic concept used to explain the beneficial effects of different industries clustering together in the same geographic area.

Contrary to previous knowledge (Reid and Lortie 2012), we also found that foundation species did not generally increase insect diversity but could have neutral and negative effects too. For instance, pollinator diversity nonlinearly increased in *A. tetraquetra* networks but did not vary in *H. spinosa*. The sign of these effects may depend on specific traits of foundation species such as how loose the cushion-like growth form is. Plants associated with *A. tetraquetra* grew and bloomed on top of its compact cushion (Appendix S1: Fig. S8). Conversely, plants associated with *H. spinosa* grew beneath its looser cushion and rarely reached the canopy (Appendix S1: Fig. S8). These differences in visibility and accessibility of plant flowers by pollinators can explain differences in the effects of *A. tetraquetra* and *H. spinosa* on pollinator

diversity. These results can be useful for managing biodiversity and ecosystem services by pollinators. They indicate that plant communities formed by foundation species *A. tetraquetra* can better support pollinator diversity and potentially increasing pollination.

Pollination networks usually show a typical nested structure (Bascompte et al. 2003) and are seldom anti-nested (but see Olesen et al. 2007). Here, we observed that network nestedness was significantly inhibited by plant facilitation in *A. tetraquetra* and *H. spinosa* networks. This means that the organization of interaction networks in subsets comprising specialist species and their more generalist partners is loosened under the facilitation conditions given by *A. tetraquetra* and *H. spinosa*. According to Bastolla et al. (2009), our results suggest that plants increased competition for pollination when occurring in multispecies assemblages with foundation species compared to growing separately. We hypothesize that increasing competition between plants for pollinators as well as with inhibition of pollinator foraging in *H. spinosa* canopy may be responsible for the observed anti-nested patterns in control networks.

Research on nonadditive effects of species interactions beyond pairwise interactions is at its infancy (Levine et al. 2017) but can substantially benefit from research on neighborhood effect. Plants can facilitate the pollination of their neighbors (Feldman et al. 2004, Ghazoul 2006, Mesgaran et al. 2017). For instance, *Raphanus raphanistrum* was more visited by pollinators and produced more seeds when growing together with other plant species than in monoculture (Ghazoul 2006). Indeed, attractive plants can increase the number of pollinator visitors to the neighborhood and indirectly increase the attractiveness of neighboring plants. This can have profound consequences for plant fitness (Mesgaran et al. 2017). In this way, beneficial effects of blooming in diverse communities that are more attractive to pollinators than species-poor communities can overcome the negative effects of competition for pollinators and pollen dispersal. Our study represents a first approach to understand how interactions within a trophic level, such as facilitation among plants for growth and survival, are coupled with interactions between trophic levels such as pollination networks. Differences between additive and control networks may be related to differences in plant density or biomass, which were not controlled in our field experiment due to logistic limitations. However, there were no differences in plant diversity and composition and we adjusted for flower diversity when calculating pollination interactions. In addition, we considered only two taxa of foundation species and including broader range of species with different growth forms would be useful to unveil more general patterns. A second limitation relates to the assumption that individual plant species have comparable chemistry when growing together and when growing with other plants (Lazaro et al. 2014). Foundation and associated species may alter each other's pollinator

attractiveness by enhancing floral reward and display (Junker et al. 2017). It is possible that plants associated with foundation species produced better nectar or more complex volatile organic compounds. This can have dramatic effects on pollinator behavior (Junker et al. 2017) and affecting pollinator visits and foraging. Changes in foraging choices by pollinators would provide a mechanistic hypothesis for the nonadditive effects and interaction rewiring observed in the current study.

In conclusion, nonadditive effects of plant interactions affected both pollinator diversity and the structure of pollination networks. We experimentally showed how interactions within trophic levels scale-up to interactions at another trophic level, ultimately shaping ecological networks. Our results imply that pollination interactions change in the presence of other competitor and facilitator plant species within the networks, shedding new light on how different networks are coupled and shaped by nonadditive effects. Understanding interaction chains can help improving management of biodiversity and ecosystem services such as pollination.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2619/suppinfo

Data Availability

All original data and R scripts used in this study will be available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.84rs783.