Facilitation and biodiversity jointly drive mutualistic networks

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ABSTRACT

1. Facilitation by legume nurse plants increase understorey diversity and support diverse ecological communities. In turn, biodiversity shapes ecological networks and supports ecosystem functioning. However, whether and how facilitation and increased biodiversity jointly influence community structure and ecosystem functioning remains unclear.

2. We performed a field experiment disentangling the relative contribution of nurse plants and increasing understorey plant diversity in driving pollination interactions to quantify the direct and indirect contribution of facilitation and diversity to ecosystem functioning. This includes analysing pollinator communities in the following treatment combinations: (i) absence and presence of nurse plants, and (ii) understorey richness with none, one and three plant species.

3. Facilitation by legume nurse plants and understorey diversity synergistically increase pollinator diversity. Our findings reflect diverse assemblages in which complementarity and cooperation among different plants result in no costs for individual species but benefits for the functioning of the community and the ecosystem. Drivers of network change are associated with increasing frequency of visits and non-additive changes in pollinator community composition and pollination niches.

4. *Synthesis* Plant–plant facilitative systems, where a nurse shrub increases understorey plant diversity, positively influences mutualistic networks via both direct nurse effects and indirect plant diversity effects. Supporting such nurse systems is crucial not only for plant diversity but also for ecosystem functioning and services.

Keywords

Biodiversity, Ecological networks, Ecosystem function and services, Multi-trophic interactions, Nurse plants, Plant–Plant–Insect interactions, Pollination, *Retama sphaerocarpa*, Synergism, Woodland

1 INTRODUCTION

Ecologists started appreciating the importance of positive species interactions for biological communities only in the last few decades (Connell & Slatyer 1977; DeAngelis et al. 1986; Hunter & Aarssen 1988; Bertness & Callaway 1994). Today, the fact that plants provide wider benefits to other species and enhance biodiversity and ecosystem functioning is a well-consolidated notion in ecology (Bruno et al., 2003; Callaway, 2007; Levin, 2009; Keddy, 2017; Ellison, 2019). Likewise, the debate around the role of diversity in the functioning and stability of ecological communities has been resolved in favour of positive biodiversity effects (Chapin et al., 2000; Hooper et al., 2005; Tilman et al., 2014; IPBES, 2019). Yet, whether and how facilitation and biodiversity jointly influence community structure and ecosystem functioning remains less clear.

Although processes underpinning facilitation may be contingent on the organisms involved and their environment (Brooker et al., 2008), as common in ecology (Lawton, 1999), facilitation is relevant to many different ecosystems (Callaway, 2007; McIntire & Fajardo, 2014; Liancourt & Dolezal 2020) beyond specific communities (e.g., cushion plants, kelp forests) and extreme environments (salt marshes, sand dunes, alpine screes). Certain species called ‘nurse plants’ can ameliorate local environmental conditions and increase biodiversity in their understorey and in the entire ecosystem (Pugnaire, 2010; Butterfield et al., 2013; Cavieres et al., 2014; Rodríguez-Echeverría et al., 2016; Ellison, 2019). By increasing both resources and biodiversity, plant facilitation can ultimately increase ecosystem functioning, such as biomass production (Wright &

Jones, 2004; Michalet & Touzard, 2010; Wright et al. 2017, Schöb et al. 2019) and the flower visitation rate of pollinators (Losapio et al., 2019). However, whether plant facilitation influences ecosystem functioning directly or indirectly through changes in biodiversity remains largely unclear. Filling this knowledge gap is crucial for understanding how biotic processes can stabilise ecosystem functioning.

Wright and colleagues (2017) proposed three main classes of facilitation mechanisms that positively contribute to ecosystem functioning: (i) indirect biotic facilitation, via reducing species-specific natural enemies (pathogens, herbivores); (ii) abiotic facilitation via nutrient enrichment, such as the legume–rhizobia symbiosis that directly increases nitrogen availability for neighbouring plants; (iii) abiotic amelioration via improving microclimatic conditions. These mechanisms are deduced from literature on biodiversity experiments carried out mainly on plant-species-richness gradient and biomass productivity in temperate meadows (Jiang, Pu & Nemergut, 2008). Thus, the potential of such biodiversity experiments to gather generalizable knowledge is limited to a small range of latitudes, systems, and ecological functions. Nevertheless, there is an increasing number of studies showing that diversity effects also work beyond plant communities (Schleuning et al., 2015; Rohr et al., 2020), and particularly across trophic levels (Losapio et al., 2020). For example, increasing plant species richness increases pollinator diversity and supports mutualistic network structure in temperate meadows (Ebeling et al. 2008; Scherber et al. 2010; Blüthgen & Klein 2011). Therefore, given that nurse plants improve both abiotic and biotic aspects of ecosystems, ultimately increasing biodiversity, and that plant diversity in turn increases pollinator diversity and ecosystem functioning, it is reasonable to hypothesize that facilitation and therein biodiversity have joint positive effects on mutualistic networks and ecosystem functioning (Fig. 1).

Here, we provide results of a study addressing this hypothesis and disentangling the relative contribution of nurse plants and increasing understorey plant diversity in driving pollination interactions. We asked the following questions: (i) What are the joint effects of nurse plants and understorey plant diversity on the pollinator community? (ii) What are the costs and benefits for the nurse plant in terms of pollination ? (iii) How do facilitation and diversity shape pollination interactions and mutualistic networks?

2 MATERIALS AND METHODS

2.1 Study system

We used a well-studied model system characterized by the nurse plant species *Retama sphaerocarpa* (L.) BOISS. (Fabaceae), a legume shrub associated with the development of "islands of fertility" under its canopy (Pugnaire et al., 1996; Schlesinger et al., 1996). Thanks to the symbiotic, mutualistic interactions with *Rhizobia* bacteria hosted in their roots, the inherent improvement of soil resources and overall amelioration of microhabitat conditions, this legume nurse plant facilitates a wide diversity of understorey plants (Moro et al., 1997; Armas, Rodríguez-Echeverría & Pugnaire, 2011; Rodríguez-Echeverría et al., 2013, 2016; Lozano et al., 2017). Furthermore, it produces copious yellow blooms pollinated by diverse insects, including small-, medium-, and large-sized Hymenoptera as well as several species of ants (Rodríguez-Riaño et al., 1999).

As understorey, we selected three annual herbaceous species that commonly grow with and without the nurse: *Matricaria chamomilla* L. (Asteraceae), *Echium plantagineum* L. (Boraginaceae), and *Carduus bourgeanus* Boiss. & Reut. (Asteraceae). *M. chamomilla* has white and yellow flowers in an open capitulum, *E. plantagineum* has purple tubular flowers along a raceme, and *C. bourgeanus* has blue flowers in a dense capitulum. These three species therefore represent a broad set of flower morphology and pollination niches.

The study was carried out in an oak (*Quercus ilex* L.) savannah in a Mediterranean-type ecosystem at the Aprisco de Las Corchuelas research station in Torrejón el Rubio, Spain (39.81337 N -6.00022 W, 350 m a.s.l., mean rainfall of 637 mm/yr. and mean annual temperature of 18 °C).

2.2 Experimental design

In order to disentangle the role of direct facilitation by the nurse from that of indirect facilitation by the nurse through increased biodiversity on pollinators, and to further examine their joint effects on mutualistic networks, a fully-factorial experimental design including the following treatments was established (Fig. 1): (i) absence (open) and presence of the legume shrub (nurse); (ii) understorey richness with one (1 sp) and three (3 sp) plant species. This design results in the four treatment combinations of open–1sp, open–3sp, nurse–1sp, and nurse–3sp. Furthermore, a nurse alone treatment (nurse–0sp), i.e. a shrub without understorey plants, was included too. By comparing mono- and poly-cultures, this design allowed us addressing the costs and benefits of facilitation as well as the complementarity of plants for pollinators. A randomised block design was adopted by grouping together the five treatments and replicating them three times in each block over four blocks, for a total of n = 60 plots. Distance between plots within the same block was approx. 1 m. Blocks were distributed randomly over an area of about 4,800 m^2.

Plant and understorey flower density were kept constant by transplanting plants in pots. Pots were kept aggregated or sparse (*c.* 30 cm apart) below the nurse or in the open. This additional factor was replicated per block. The same pots of understorey plants were used for all blocks over two consecutive days before being replenished with fresh blooms. In the nurse alone treatment with no understorey species, three empty pots with only soil were placed under the shrub to control for any potential effect of the pots. For the nurse treatments, shrubs were chosen of approx. the same size (height 127–178 cm and width 125–220 cm). An area of 1 m^2 at 1 m height was used as the pollinator observation area in each shrub. Flowers of the surrounding vegetation within at least 1 m around each shrub and open area were cleared.

Flower visitation was considered as a proxy for the ecosystem function of pollination (Schleuning et al., 2015; IPBES, 2019). Flower visits were documented by sampling, identifying, and recording all insects visiting the flowers of each plant in each plot. Observations were conducted between 9 AM and 7 PM over eight days between 1 May and 14 May 2017, covering the blooming phase of the four plant species. Each plot was observed during three slots of 20 min. randomly allocated over the day. Nurse plants and corresponding open plots have been observed simultaneously, reducing the disturbing effects of changing weather conditions within blocks. Each block was sampled completely within two days. Pollinators were identified at the species level whenever possible, otherwise to the genus. Specimens are conserved in 90% alcohol at our institution collections.

2.3 Data analysis

To answer the first question, we calculated the abundance and richness of pollinators in each plot, i.e., at the community level. We assessed the individual and combined effects of facilitation (nurse presence vs absence) and diversity (understorey species richness) on pollinator abundance and richness (two separate models) by means of Zero-inflated Generalized Linear Mixed Modelling (Zi-GLMM) with a negative binomial distribution (Brooks et al., 2017). Understorey aggregation was included as additional factor. Plant species composition and plot nested within block were considered as random effects.

To answer the second question, we calculated flower visits for each single plant species in each plot and conducted cost–benefit analysis. For understorey plants, we assessed the individual and combined effects of nurse shrubs and understorey species richness on pollinator abundance by means of Zi-GLMM with a negative binomial distribution. Understorey aggregation was included as additional factor. Plant species identity and plot nested within block were considered as random effects. For nurse shrubs, we assessed the effects of understorey species richness (nurse alone, 1 species and 3 species; second-degree polynomial) on pollinator abundance by means of Zi-GLMM with a negative binomial distribution. Understorey aggregation was included as additional covariate. Understorey composition and plot nested within block were considered as random effects.

To answer the third question, we used a framework based on the variance partitioning of biodiversity effects (Loreau and Hector 2001) for the pollinator community (Losapio et al., 2020). This framework allows comparing the net impact of a diverse plant community on flower visits, distinguishing between complementarity and selection effects (Loreau and Hector 2001; Wright et al. 2017; Losapio et al., 2020). First, we calculated complementarity effects (CE) and selection effects (SE) among understorey species as: $\mathrm{CE} = 3\ \overline{\frac{Y_{mc}}{M_{mc}} - 1, \frac{Y_{ep}}{M_{ep}} - 1, \frac{Y_{cb}}{M_{cb}} - 1}\ \overline{M_{mc}, M_{ep}, M_{cb}}$, and $\mathrm{SE} = 3\ cov\ (\overline{\frac{Y_{mc}}{M_{mc}} - 1, \frac{Y_{ep}}{M_{ep}} - 1, \frac{Y_{cb}}{M_{cb}} - 1}, \overline{M_{mc}, M_{ep}, M_{cb}})$, where Y and M indicate flower visits in polyculture (three understorey species) and monoculture (one understorey species), respectively, for each understorey plant species (*M. chamomilla*, *E. plantagineum*, *C. bourgeanus*). These effects were calculated both in the absence and presence of nurse shrubs. This way, we tested the impact of plant facilitation on CE and SE. Then, the diversity effects were tested in response to nurse presence, effect type, and their interaction using a linear model. Second, we calculated CE and SE between nurse shrubs and understorey species. This way, nurse and understorey were considered as two distinct functional groups. These functional diversity effects were calculated as:

$\mathrm{CE} = 2\,\overline{\frac{Y_{ns}}{M_{ns}} - 1, \frac{Y_{us}}{M_{us}} - 1}\;\overline{M_{ns}, M_{us}}$, and $\mathrm{SE} = 2\,cov\,(\frac{Y_{ns}}{ns} - 1, \frac{Y_{us}}{M_{us}} - 1, \overline{M_{ns}, M_{us}})$, where Y and M indicate flower visits in polyculture (two functional diversity groups of nurse and understorey) and monoculture (nurse and understorey alone), respectively. These effects were calculated with both one and three understorey species (nurse–1sp and open–1sp; nurse–3sp and open–3sp). This way, we tested how CE and SE change with plant diversity. Then, the diversity effects were tested in response to understorey richness (categorical), effect type, and their interaction using a linear model.

To answer the third question, we built mutualistic networks between the four plant species and each of their pollinator species (or genus) according to the additive matrix framework (Losapio et al., 2019). This approach consists of building and comparing observed networks (hereafter, ‘synergistic’) with ‘additive’ networks. ‘Synergistic’ networks are built using the plant–pollinator interactions data collected from the empirical plant community, here composed by the nurse shrub and the three understorey species. Instead, ‘additive’ networks are built using data collected from the four treatments of nurse shrub and understorey species monocultures and pooling plant–pollinator interactions into a single ‘additive’ matrix.

To quantify network structure, we measured network eigenvector centrality (Bonacich, 1987; Csardi & Nepusz, 2006). This metric quantifies the extent to which plant species with many pollinators are connected to pollinators that visit few species or poorly connected plants interact with a few central pollinators. Then, to understand the drivers of differences in mutualistic networks, we measured the dissimilarity between the networks using the framework of beta-diversity of species interactions (Poisot, 2016). In particular, we considered the dissimilarity in species composition and pairwise plant–pollinator interactions. In this case, networks were considered at the block level. Network dissimilarity was calculated within 'additive' networks, within 'synergistic' networks, and between 'additive' and 'synergistic' networks. Differences among networks were tested in response to the dissimilarity index (species or interactions), dissimilarity within networks nested within dissimilarity between networks, and their interaction using a linear model.

Statistical results are reported in terms of variances explained, using type-II ANOVA (Fox & Weisberg, 2019), and parameter estimates with 95% Confidence Interval. In case of significant statistical interactions, contrasts among factor combinations were computed using estimated marginal means (Lenth, 2020).

3 RESULTS

3.1 Pollinator community

We found that both nurse presence ($P < 0.001$) and diversity ($P = 0.002$) significantly explain differences in visitor abundance at the community level (Fig. 2a), whereas aggregation and the interaction between nurse presence and diversity were not significant. In particular, the nurse shrub increases flower visitor abundance by 68% compared to open (β, 95%CI = 1.72, 0.99–2.45). Furthermore, increasing understorey plant diversity from one to three species increases flower visitor abundance by 19% (0.56, 0.22–2.92).

Similarly, nurse presence ($P < 0.001$), diversity ($P = 0.002$) and their statistical interaction ($P = 0.040$) significantly influence pollinator species richness (Fig. 2b), whereas aggregation was not significant. On average, the presence of the nurse shrub increases the richness of the pollinator community by 74% (1.6, 1.07–2.13), and increasing understorey plant diversity from one to three species increases richness by 24% (0.34, 0.15–0.54). Furthermore, nurse presence and understorey diversity jointly influence pollinator richness, being the effects of diversity stronger in open (c = 0.69 ± 0.20 SE, P = 0.005) than underneath the nurse canopy (c = 0.19 ± 0.14 SE, P = 0.495), and the effects of nurse presence stronger at low diversity (c = 1.35 ± 0.17, P < 0.001) than high diversity (c = 0.86 ± 0.17 SE, P < 0.001).

3.2 Benefits and costs

We then explored the effects of facilitation and diversity on flower visitation rate per each species. Considering understorey plants, diversity had significant effects on flower visits (P < 0.001), which was independent of aggregation, nurse presence or its interaction (Fig. 3a). In particular, increasing understorey diversity increased the number of flower visits on each understorey species by 34% (0.40, 0.14–0.54). Variance among species was low (0.013).

Considering the legume nurse shrub, both aggregation and diversity significantly influenced visitation rate (P = 0.045 and P = 0.002, respectively). In particular, aggregating understorey plants increased visitor abundance for the nurse shrub by 10% (0.39, 0.01–0.76). Understorey diversity had non-linear effects on nurse's visitors (Fig. 3b), being positive only at high richness (quadratic term 2.28, 0.98–3.59).

3.3 Complementarity and selection effects

We then explored diversity effects (i.e. complementarity and selection effects) among understorey species (Fig. 4a) and between nurse and understorey (Fig. 4b). In the case of understorey species richness, we found that diversity effects were independent of nurse shrubs but significantly varied between complementarity and selection effects (P < 0.001), since selection effects were more negative than complementarity effects positive (Fig. 4a). In particular, complementarity effects were marginally positive in the absence and presence of nurse shrubs (499, -33.1–1031; 517, -15.5–1049), respectively, while selection effects were negative in both cases (-754, -1286.3– -222; -771, -1302.9– -238).

In the case of the nurse–understorey combination, diversity effects between nurse and understorey plants changed with understorey species richness (P = 0.033) depending on effect type (P = 0.009). While complementarity effects significantly increased with increasing understorey richness (c = 160.0 ± 41.1 SE, P = 0.002), selection effects remained the same (c = 20.1 ± 41.4 SE, P = 0.495). Furthermore, complementarity effects were negative and positive at low and high richness (-124.6, -188.3– -60.89; 36.2, -27.5–99.93), respectively, while selection effects were always marginally negative (-38.5, -102.2–25.26; -58.6, -122.3–5.14).

3.4 Network change

Finally, we explored mutualistic network centrality and dissimilarity between additive and synergistic networks. We found that synergistic networks were significantly less centralized than additive networks (β = -0.35, P < 0.001, Fig. 5). Considering components of network dissimilarity, species turnover was twice as high as interaction change overall (c = 0.20 ± 0.02 SE, P < 0.002), with dissimilarity in interaction change between synergistic networks being lower relative to dissimilarity in species composition between additive networks (-0.14, -0.25– -0.02).

4 DISCUSSION

Species interactions and biodiversity play a crucial role in shaping ecological networks and supporting ecosystem functioning, yet their joint effects remain poorly understood. Now we provide new evidence for the mingled consequences of plant facilitation and diversity for mutualistic networks of pollination, a key ecosystem function. The results of our field experiment indicate that facilitation by legume nurse shrubs and understorey diversity synergistically increase the diversity of pollinators. Our findings reflect diverse assemblages in which complementarity and cooperation among different plants result in no costs for individual species but benefits for the functioning of the community and the ecosystem.

4.1 Community-scale benefits

Results support the hypotheses that facilitation and biodiversity jointly influence mutualistic networks and ecosystem functions, as both nurse shrub and understorey diversity increase pollinator abundance and richness at the community level.

Facilitation can positively influence ecological networks beyond plant communities, including pollination networks (Losapio et al., 2019), arthropod food-webs (van der Zee et al., 2016), mammal communities (Lortie et al., 2016), and soil microorganisms (Rodríguez-Echeverría et al., 2013). Notably, benefits of facilitation involve not only the plant community itself but also scale up to flower visitors, whose diversity increases in nurse–understorey assemblages. Thus, the amelioration of biophysical environment by legume nurse shrubs favours both understorey species (Pugnaire 2010), directly via microhabitat improvement and indirectly via enhanced pollination, the plant community as a whole as well as the pollinator network. Underlying mechanisms may be enhanced floral display via increasing community-level attractiveness to generalist pollinators (Losapio et al. 2019), i.e., 'cluster effect' (Krugman, 1991), and service sharing (McIntire & Fajardo, 2014). Moreover, enhanced floral resources via soil symbionts of the legume nurse shrub (Harris, 2009; Rodríguez-Echeverría et al., 2016) may also be responsible for improving floral attractiveness in natural conditions.

Besides nurse shrub presence, increasing understorey diversity increases pollinator diversity, as the higher the floral diversity the higher the availability of resources for pollinators in polyculture as compared to monoculture. These results are consistent with previous studies showing that plant diversity, along with the co-varying factors including blossom cover and presence of particularly attractive flowering species, enhances both the frequency and the temporal stability of pollinator visits (Ebeling et al., 2008). In addition, flower visits increase with plant diversity when diverse flower displays increase the duration of flower provision (Fornoff et al., 2017) and widen pollination niches (Losapio et al., 2020). Since plant and flower density were kept constant in our experiment, the positive effects of understorey diversity on ecosystem functions are mainly driven by pollination niche complementarity and loss of poorly-attractive species, as discussed in the paragraph below (4.2).

Notably, the combination of facilitation and diversity effects produce even greater benefits for mutualistic networks than expected by these two factors alone. In fact, adding more understorey species (at constant plant and flower density) produce stronger effects on pollinator diversity in the absence of nurse shrubs as compared to their presence. That is, facilitation and diversity synergistically interact to influence ecosystem functioning. This is most likely due to the overwhelming facilitative effects of nurse shrubs and the non-linear nature of community assembly processes. The presence of nurse shrubs seems more important at low diversity, while increasing diversity seems more relevant in the absence of facilitation. Most importantly, our results show that plant–plant facilitation is an important driver of mutualistic networks and ecosystem functioning, both directly and indirectly via increasing biodiversity.

Cost–benefit analysis reveals that species-specific pollination facilitation results in neutral net effects for both nurse and understorey species and positive net effects of biodiversity. That is, the benefits of facilitation for the whole community come at no costs for the individual species. It is not surprising that nurse shrubs do not necessarily increase flower visitation of understorey species, as the outcome of specific facilitation mechanisms is often context-dependent and varies in the short term (Montesinos-Navarro et al., 2019). In fact, facilitation for vegetative reproduction (establishment, growth, survival) can be independent from facilitation for sexual reproduction (Losapio et al., 2019). Interesting enough, the positive effects of biodiversity scale from communities to single species since there is a correspondence between increasing ecosystem functioning and increasing species visits. This is not always the case for biodiversity experiments, where an increase in community productivity does not necessarily follow an increase in species-specific biomass (Tilman et al., 2014).

4.2 Complementarity and selection effects

The current understanding of the relationships between biodiversity and ecosystem functioning comes primarily from studies focusing on the effects of plant species richness on biomass production in temperate meadows (Jiang et al., 2008). While competition is often claimed to play a role in such system, facilitation is overlooked or lumped within several less explicitly defined processes as complementarity effects (Blüthgen & Klein 2011; Wright et al., 2017). The experimental framework we adopted here allows us manipulating both taxonomic and functional diversity in combination with facilitation, then measuring complementarity among understorey species as well as between nurse shrubs and understorey plants.

Our results indicate positive complementarity effects among understorey species. Furthermore, complementarity between nurse and understorey species increases with diversity. Results also indicate negative selection effects, suggesting that species with generally few pollinators benefit the most in the polyculture (understorey species), while a species (possibly the nurse plant) with generally lots of pollinators does not. These provide new evidence for a novel facilitation process based on community-scale facilitation (Callaway, 2007; Liancourt & Dolezal 2020) and on the 'cluster effect' (Krugman, 1991; Losapio et al., 2019) at different trophic levels: diverse flower assemblages including nurse shrubs are more attractive than monocultures thanks to increased visibility of the community as a whole for attracting a wider spectrum of visitors.

This way, being part of the polyculture cluster (nurse shrub with diverse understorey) would increase the chances of being visited, and eventually pollinated. Joint effects of diversity and community-scale facilitation involve not only the plant community itself but also flower visitors, whose diversity increased in nurse–understorey assemblages. Thus, the amelioration of the biophysical environment by legume nurse shrubs favours understorey species (Pugnaire 2010), directly via microhabitat improvement and indirectly via enhanced pollination, but also the plant community as a whole and its ecosystem functions.

4.3 Network change

By means of the additive matrix framework (Losapio et al., 2019), we compared synergistic networks that emerge from the plant community as a whole with additive networks that result from pooling plant species as separate components. These two networks appear to be very different, highlighting the non-additivity of nurse and understorey plants. This shows that interactions among plants influence interactions between plants and pollinators. In particular, facilitative interactions among nurse and understorey plants influence pollination networks by changing the identity and frequency of flower visitors. Such nonadditive interactions change network structure, making the network more de-centralised than expected by additive effects, which may ultimately improve the overall resistance and stability of pollinator communities (Blüthgen & Klein 2011). Furthermore, our results show that synergistic networks were more similar among each other in terms of species interactions as compared to the higher dissimilarity of species interactions observed among 'additive' networks. Drivers of network change are associated with increasing frequency of visits and potentially pollinator population density, thus affecting interaction strength, as well as changes in floral attractiveness and pollination niches, which ultimately promote species turnover and interaction rewiring.

Notice that this is different from a case of pollination facilitation (Feldman et al., 2004; Gazhoul, 2006; Braun & Lortie 2019), where the presence of a plant increases pollination of a neighbour, but the two do not always interact directly, e.g., facilitating germination and survival (Losapio and Schöb 2020). In the present case study, plant species are interacting directly via changes in microhabitat conditions and soil symbionts. Furthermore, we now show that they also interact indirectly via pollination networks.

In conclusion, our study shows that plant–plant facilitative systems where a nurse shrub increases understorey plant diversity positively influences pollination networks via both direct nurse effects and indirect plant diversity effects.

Acknowledgements

GL and CS are grateful for financial support by the Swiss National Science Foundation (P2ZHP3_187938, PZ00P3_148261 and PP00P3_170645).

Authors' contributions

GL and CS designed the study; EN conducted the experiment; LC, XE, CG, JO, AP and DS identified the specimens; GL analysed the data and wrote the manuscript with inputs from CS. All authors commented and approved the final publication.

The authors have declared no competing interest.

Data availability

The dataset will be published in the in the Dryad Digital Repository upon manuscript acceptance.

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Figures and tables

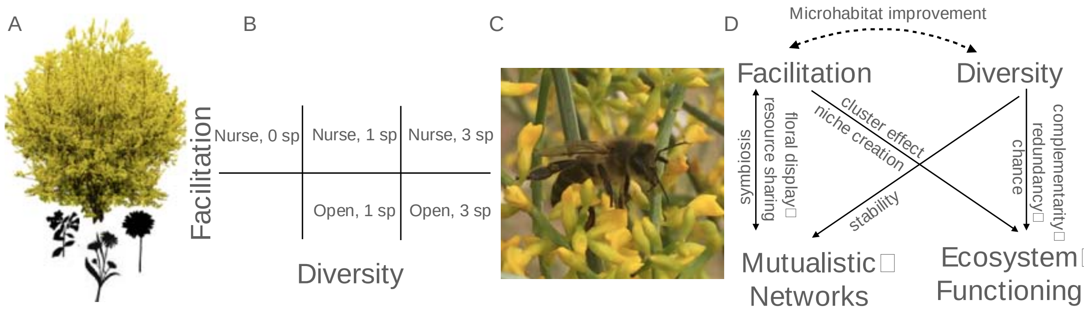
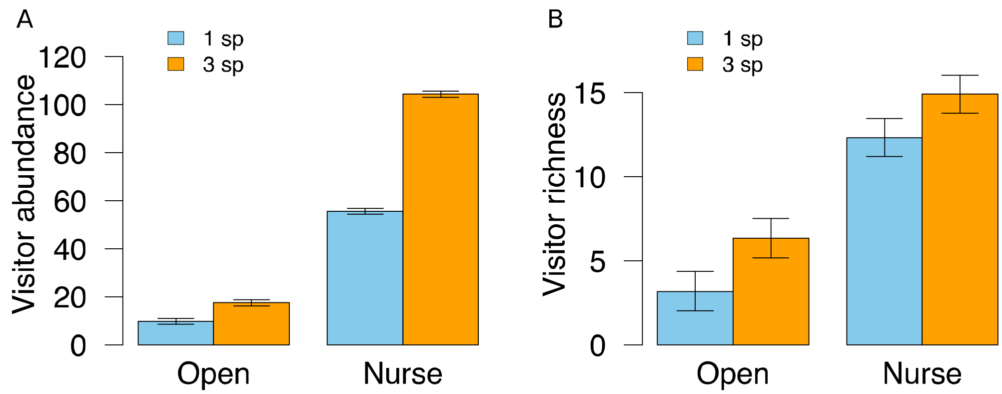


Fig. 1 Conceptual framework and experimental design. (A) A legume nurse shrub (*Retama sphaerocarpa*) facilitates diverse herbaceous plant species in the understorey. (B) To examine the joint effects of plant facilitation and biodiversity change on mutualistic networks, the experimental design includes the treatments of nurse presence/absence and understorey species richness. Plant and flower density of understorey species were kept constant. Furthermore, a nurse alone treatment (i.e., shrub without understorey plants) was included. (C) We then examined the response of pollination interactions, such as those between *Apis mellifera* and *Retama sphaerocarpa*. (D) Process pathways among facilitation, diversity, mutualistic networks and ecosystem functioning.

563 

564 **Fig. 2** Effects of facilitation (open vs nurse) and biodiversity (1 vs 3 species) on
565 abundance (A) and richness (B) of the pollinator community (i.e., flower visitors) per
566 plot. Bars indicate SE.

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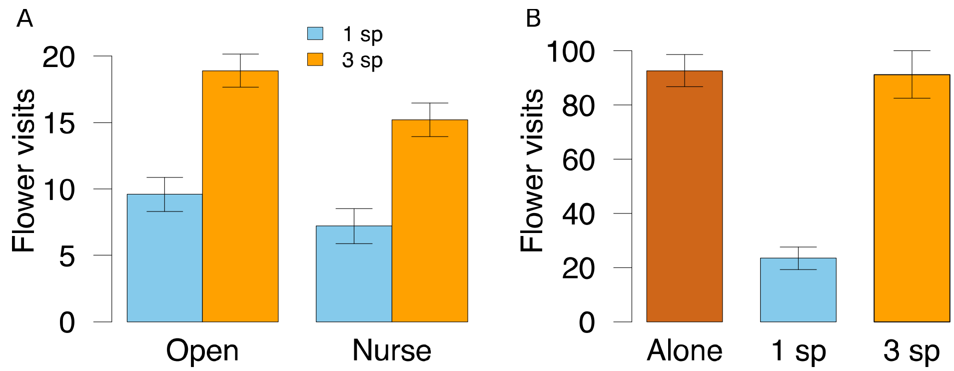

Fig. 3 Cost and benefit analysis of facilitation (open vs nurse) and biodiversity (1 vs 3 understorey species) for understorey plants (A) and nurse shrubs (B) in each plot. Bars indicate SE.

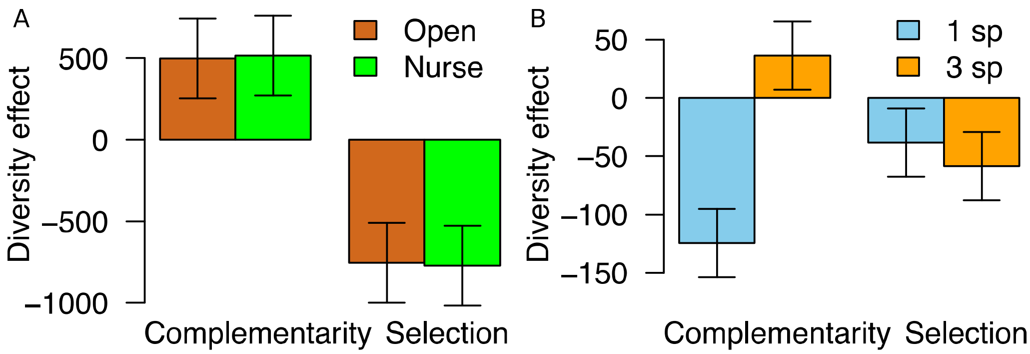

Fig. 4 Consequences of facilitation (open vs nurse) for complementarity and selection effects among understorey species (A). Complementarity and selection effects between nurse plants and understorey species (B). Bars indicate SE.

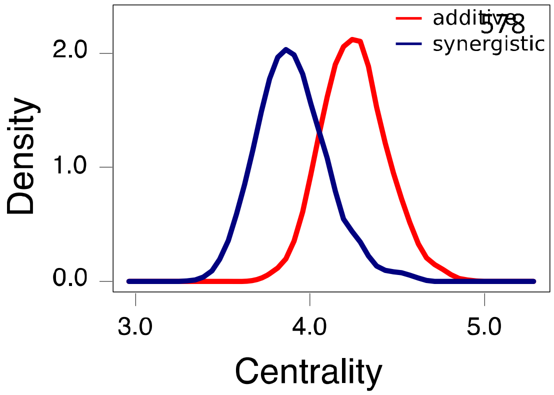

Fig. 5 Network centrality of additive networks (red) and synergistic networks (blue).