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An experimental approach to assessing the impact of ecosystem engineers on biodiversity and ecosystem functions

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Abstract

Plants acting as ecosystem engineers create habitats and facilitate biodiversity maintenance within plant communities. Furthermore, biodiversity research has demonstrated that plant diversity enhances the productivity and functioning of ecosystems. However, these two fields of research developed in parallel and independent from one another, with the consequence that little is known about the role of ecosystem engineers in the relationship between biodiversity and ecosystem functioning across trophic levels. Here, we present an experimental framework to study this relationship. We combine facilitation by plants acting as ecosystem engineers with plant–insect interaction analysis and variance partitioning of biodiversity effects. We present a case-study experiment in which facilitation by a cushion-plant species and a dwarf-shrub species as ecosystem engineers increases positive effects of plant functional diversity (ecosystem engineers and associated plants) on ecosystem functioning (flower visitation rate). The experiment, conducted in the field during a single alpine flowering season, included the following treatments: 1) removal of plant species associated with ecosystem engineers, 2) exclusion (covering) of ecosystem engineer flowers, and 3) control, i.e. natural patches of ecosystem engineers and associated plant species. We found both positive and negative associational effects between plants depending on ecosystem engineer identity, indicating both pollination facilitation and interference. In both cases patches supported by ecosystem engineers increased phylogenetic and functional diversity of flower visitors. Furthermore, complementarity effects between engineers and associated plants were positive for flower visitation rates. Our study reveals that plant facilitation can enhance the strength of biodiversity–ecosystem functioning relationships, with complementarity between plants for attracting more and diverse flower visitors being the likely driver. A potential mechanism is that synergy and complementarity between engineers and associated plants increase attractiveness for shared visitors and widen pollination niches. In synthesis, facilitation among plants can scale up to a full network, supporting ecosystem functioning both directly via microhabitat amelioration and indirectly via diversity effects.

Key words: biodiversity change; complementarity effect; ecosystem functioning; facilitation; functional diversity; multitrophic interactions; phylogenetic diversity; plant–plant–insect networks

Introduction

Biological diversity is critical to the functioning and stability of ecosystems (Schmid et al. 2002; Hooper et al. 2005; Tilman et al. 2014), but human impact on the environment accelerates biodiversity loss (Chapin et al. 2000; Naeem et al. 2012). These changes also threaten to disrupt biotic interactions that support critical ecosystem functions such as mutualism and pollination (Tylianakis et al. 2008; Winfree et al. 2018; Bascompte et al. 2019). To address these challenges, it is crucial to understand how species interactions enhance the persistence of natural populations and support ecological systems and their functions (Valiente-Banuet et al. 2015; Losapio & Schöb 2017). Yet, joint consequences of species interactions and changing biodiversity for ecosystem functioning remain poorly understood.

Organisms acting as ecosystem engineers, such as kelps or trees, play critical roles in biological communities by increasing habitat complexity (Jones et al. 1994; Stachowicz 2001; Ellison 2005), creating new biotope space (Hutchinson 1978; Odling-Smee et al., 2003; Schöb et al. 2012), and facilitating biodiversity maintenance (Wright et al. 2006; He et al. 2013; Bulleri et al. 2018). Among plants, ecosystem engineers can ameliorate environmental conditions, decrease stress and disturbance, and ultimately support the ecological network (Cavieres et al. 2014; Losapio et al. 2018; Thomsen et al. 2018; Ellison 2019). These positive effects can provide benefits to associated plant species by facilitating their establishment, growth, survival and reproduction (Bertness and Callaway 1994; Bruno et al. 2003; Michalet et al. 2006; McIntire & Fajardo 2014; Schöb et al. 2014a; Losapio et al. 2018), thus increasing plant diversity at the community level (Armas et al. 2011; Cavieres et al. 2014; Kikvidze et al. 2015). Besides interactions between species within plant communities, little is known about the cascading effects of plant-to-plant facilitation across trophic levels (Bronstein 2009; Lortie et al. 2016; Lozano et al. 2017; Braun & Lortie 2019; Losapio et al. 2019).

Facilitation by plants acting as ecosystem engineers can influence the structure and diversity of ecological communities other than plants. For instance, the cushion plant *Silene acaulis* is an ecosystem engineer that can host higher diversity of arthropod species than non-cushion plants in alpine ecosystems (Reid & Lortie 2012). In a similar fashion, the evergreen shrub *Larrea tridentata* supports more diverse arthropod communities than open areas in the Mojave Desert (Ruttan et al. 2016). In addition to direct effects, facilitation cascades can arise when ecosystem engineers facilitate another species and, collectively, they increase habitat complexity and quality, further enhancing biodiversity (Altieri et al. 2007). In this way oak trees facilitate epiphytic plants and, in turn, increase abundance and diversity of invertebrates (Angelini & Silliman 2014).

Similarly, Losapio et al. (2019) recently found that facilitation by cushion plants (*Arenaria tetraquetra*) acting as ecosystem engineers increases pollinator diversity and supports ecological network structure in a synergistic way. Nevertheless, little is known about the extent to which plant facilitation by ecosystem engineers modulates the effects of plant functional diversity on ecosystem functioning and the specific mechanisms involved (but see Badano & Marquet 2009). For example, it is possible that positive effects of plant facilitation by ecosystem engineers scale up to flower visitor diversity and distant trophic levels strengthening the relationship between biodiversity and ecosystem functioning (BEF).

The classic approach to study plant interactions is examining dependent plants in the presence and absence of neighbors (Grace & Tilman 1990; Callaway 2007). Specifically, by comparing the germination, establishment, growth, reproduction, survival, population size, diversity, or traits of dependent plants with and without neighboring plants, we can quantify the effects of competition and facilitation (Callaway et al. 2002; Schöb et al. 2012; Hart et al. 2018). A positive response to the presence of neighbors, such as ecosystem engineers, supports hypotheses focused on direct and indirect facilitative effects, whereas a negative response is consistent with predictions from competitive effects. Furthermore, ecosystem engineers can enhance ecosystem functions directly through improvement of microhabitat conditions and resources as well as indirectly from increased community-level plant diversity, including functional, genetic, and taxonomic diversity (Wright & Jones 2004; McIntire & Fajardo 2014). Nevertheless, using only the classic pairwise approach it remains difficult to disentangle direct effects of species interactions on ecosystem functions from indirect effects arising from biodiversity change. In cases where experiments are not feasible, structural equation modeling (Grace & Keeley 2006; Shipley 2009; Lefcheck 2016) may help inferring relationships among species interactions, biodiversity and ecosystem functions controlling for the many confounding factors. In combination with SEM and whenever feasible, experimental manipulation is required for understanding the multiple facets of causes and consequences of diversity change, but we still have a limited knowledge of direct and indirect effects involving interaction chains across trophic levels, and their consequences for BEF relationships.

To address this knowledge gap and contributing to resolve the question of whether and how facilitation affects BEF relationships, we suggest an experimental framework that combines methods from plant–plant interaction and from biodiversity experiments (Fig. 1). The aim of disentangling the effect of individual species from the effect of community-level diversity on

ecosystem functions is common to biodiversity experiments (Schmid et al. 2002; Tilman et al. 2014), where study designs and analytical frameworks have been developed to tackle this issue. By means of experiments that include each focal species in isolation as well as in communities that vary in species richness and composition, the impact of each species on response variables can be compared with the impact of a combination of species. The most commonly used analytical framework for these experiments is the additive partitioning of biodiversity effects (Loreau and Hector 2001), which allows for comparisons of the net impact of a diverse community versus effects of individual species on a response variable. This analytical approach also allows disentangling complementarity effects from sampling effects, where the effects of biodiversity stem from species complementarity or from the increased probability of hosting a species with a particularly strong or weak impact, respectively (Loreau and Hector 2001; Hooper et al. 2005; Wright et al. 2017; Barry et al. 2019).

Here, we consider ecosystem engineers and associated plants as two distinct functional diversity levels and examine ecosystem engineers and associated plants flowering alone and together, respectively. The analytical procedure consists of coupling plant–insect interaction analysis with variance partitioning of biodiversity effects for flower visitation rates, considered as a proxy for the ecosystem service of pollination. In this way we can quantify the complementarity and selection effects of functional diversity on flower visitors and describe how the ecosystem engineer modulates these biodiversity effects across trophic levels. Ecosystem engineers and their associated plants will facilitate and complement each other for flower visitors when both are visited by more insects when growing together than when growing alone (Fig. 1). We propose two non-exclusive mechanisms: (1) increasing overall attractiveness for flower visitors, particularly rare ones (see the beetle in Fig. 1), i.e., niche differentiation, and (2) increasing complementarity for shared visitors (see the bumblebee and the butterfly in Fig. 1), i.e., flower-visit facilitation.

We hypothesize that the association between ecosystem engineers and different plants increases visitor diversity and visitation rates via complementarity effects. We applied our framework to two ecosystem engineer species (a cushion-plant species and a dwarf-shrub species, Fig. 1) and associated plant communities to answer the following questions: (1) do ecosystem engineers facilitate flower visits to associated plants? (2) Does plant–plant facilitation increase functional and phylogenetic diversity of flower visitors? (3) Does plant–plant facilitation increase ecosystem functioning (i.e., flower visitation rates) via complementarity or selection effects?

Materials and methods

Study site and ecosystem engineers

The study was carried out in a dry, Mediterranean alpine ecosystem in Sierra Nevada, Spain (Loma del Mulhacén, 3200 m a.s.l.). This is a well-studied model ecosystem characterized by vegetation patches that are structured by two sparsely-distributed plants that act as ecosystem engineers: *Arenaria tetraquetra* ssp. *amabilis* (Bory) H.Lindb. (Caryophyllaceae) and *Hormathophylla spinosa* L. (Brassicaceae). The engineer *Arenaria tetraquetra* is a cushion plant with compact, small and dense branches (Blanca et al. 2011, Schöb et al. 2012) and white actinomorphic flowers visited by more than twenty-five pollinator species (Gómez et al. 1996; Losapio et al. 2019). Associated plant species grow and flower on top of its canopy (Fig. 1). *Hormathophylla spinosa* is a dwarf shrub with spiny branches and small laves (Blanca et al. 2011) and has copious actinomorphic purple flowers visited by more than twenty pollinator species (Losapio et al. 2019). Associated plant species grow and flower underneath its canopy (Fig. 1).

Experimental design

After surveying the plant community (Appendix S1: Section S1, Methods), we selected a pool of plant species for carrying out the removal experiment, which consisted of the eight most-frequently associated plant species: *Anthyllis vulneraria* ssp. *pseudoarundana* H. Lindb. (Fabaceae), *Chaenorrhinum glareosum* (Boiss. & Reut.) Willk. (Plantaginaceae), *Crepis oporinoides* Boiss. (Asteraceae), *Jasione amethystina* Lag. & Rodr (Campanulaceae), *Leontodon boryi* Boiss. (Asteraceae), *Leucanthemopsis pectinata* (L.) López & Jarvis (Asteraceae), *Lotus corniculatus* subsp. *glacialis* (Boiss.) Valdés (Fabaceae) and *Sideritis glacialis* Boiss (Lamiaceae).

The removal experiment consisted of the three following treatments: 1) removal (clipping aboveground parts) of all associated plants within and around randomly selected individuals of ecosystem engineers, 2) flower exclusion (covering with stones) of ecosystem engineers nearby associated plants, and 3) no removal (i.e., patches with naturally co-occurring ecosystem engineers and associated plants). In this way we ensured to remove the effects of ecosystem engineer flowers, ignoring other abiotic effects, without compromising the integrity of examined organisms and ecosystem (a protected National Park).

Each treatment consisted of 20 x 20 cm standard plots, a size that reflects the fine spatial scale of plant facilitation in this alpine environment (Schöb et al. 2012, Schöb et al. 2013) as well as the intimacy of plant–pollinator interactions (Thomson & Chittka 2001, Losapio et al. 2019).

Given the fine spatial resolution of our experiment, we were interested in assessing the insect response at the community scale (i.e., flower visitors) rather than at the landscape scale (i.e., species pool).

We followed a randomized-block design, where each block included the three treatments for each ecosystem engineer species. The distance between plots within blocks was 50–100 cm, which was considered sufficient for undisturbed insect choice (Thomson & Chittka 2001). We kept associated plant species composition and diversity as similar as possible across blocks (Losapio et al. 2019). In total, 28 blocks, 14 blocks for *A. tetraquetra* and 14 blocks for *H. spinosa*, were established within a relatively homogeneous area of about 1 ha ($n = 84$).

Plant–visitor interactions

We surveyed flower visitors over the course of an entire alpine flowering season, from beginning of flowering to petal falling, during July 2015 (Losapio et al. 2019). Species interactions were surveyed by directly observing and sampling flower visitors to flowers (plant species) in each plot. Blocks were randomly sampled between 10 am and 5.30 pm for 20 min (5 min break between rounds). We followed a matched 'pairs' design and sampled three plots within each block at the same time in order to exclude variation within blocks due to changing weather conditions and flower visitor activity. Then, blocks were sampled following a stratified random design. Each day we sampled 14 blocks, completing sampling of all 28 blocks over two consecutive days each time. We ensured that each block was sampled at each time of the day, in a random order, for 6–9 times (blocks were dismissed once petals started falling). In total, we performed 204 sampling rounds over 15 sampling days (from 6 July 2015 – 27 July 2015), covering the whole flowering phase of examined alpine plants (Appendix S1: Table S1).

Data were subsequently pooled for each plant species at the plot level ($n = 84$). Flower visitors were identified at the species level whenever possible, otherwise to genus or family (Appendix S1: Table S1). Afterwards, we classified flower visitors on the basis of life history by expert knowledge into the following trophic guilds (i.e., functional groups): pollinators, herbivores, scavengers, predators and parasitoids (Appendix S1: Table S2). These functional groups reflect the feeding behavior of the adult stage, the one that is observed interacting directly with flowers, rather than the entire life cycle. For instance, butterflies were considered as pollinators (adult stage) rather than as herbivores (larval stage). Since we exclusively observed

visits to flowers, individuals and species classified as pollinators may not all do pollination successfully and non-pollinators may do some pollination.

Data analysis

We first tested the effects of the two plant species acting as ecosystem engineers on (1) the density and (2) diversity of associated plant species. To model the density of associated plants across microhabitats, we used a generalized linear model (GLM) with Poisson distribution with the abundance of individual plant species as dependent variable and the type of microhabitat as independent variable (categorical with open, *A. tetraquetra* and *H. spinosa*). To model the diversity of associated plants across microhabitats, we first fitted species richness as a function of the number of individuals using a Poisson GLM. Then, we modelled the residuals of this model as a function of microhabitat using a linear model (LM), therefore accounting for and removing direct effects of density on diversity.

To answer the second question, we tested the effects of the presence of ecosystem engineers on the number of flower visitors to associated plant species. We used a Poisson mixed-effects GLM with visitor abundance as a function of ecosystem engineer presence (categorical variable with two levels), ecosystem engineer identity (categorical variable with two levels) and their interaction; the abundance of flowers of associated plants was fitted first as further covariate and blocks were random effects.

We then tested the effects of plant removal treatments on (1) visitor phylogenetic diversity, and (2) visitor functional diversity. To do so, we first constructed a phylogenetic tree with the relationships among all 75 sampled visitors taxa (Appendix S1: Fig. S1) using NCBI taxonomy (https://www.ncbi.nlm.nih.gov/Taxonomy/CommonTree/wwwcmt.cgi). We then measured phylogenetic structure using abundance-weighted mean phylogenetic distance (MPD) among all visitor in a plot (Kembel et al. 2010). We considered the standardized effect size of MPD as z-MPD $= (^{\mathrm{MPD_{obs}}} - \overline{\mathrm{MPD}}_{\mathrm{random}}/\sigma_{\mathrm{random}})$ by comparing the observed values with the mean and standard deviation of MPD from 99 random communities generated by randomizing the identity of visitor taxa occurring in the plots (Kembel et al. 2010).

We used linear mixed models (LMMs) to test the response of phylogenetic diversity to removal treatments (categorical variable with three levels), ecosystem engineer species (categorical variable with two levels), and their statistical interaction (fixed effects); plant species

richness (i.e., number of subordinate plant species) and flower density (i.e., number of flowers per plot) were included as fixed effects and fitted first; blocks were random effects.

Furthermore, we tested whether visitor functional diversity differed among removal treatments and ecosystem engineer species. We calculated the diversity of visitor functional groups using the Shannon index of guild abundance. Visitor diversity was standardized by flower abundance per plot. We used the same LMM structure to test the response of functional diversity to removal treatment as we did for the previous analysis of phylogenetic diversity.

We proceeded with measuring the diversity effects of plant–plant facilitation on ecosystem functioning. Flower visitation rate was used as a measure of ecosystem functioning given the biological functions of flower visitors for pollination and hence for fruit production (Winfree et al. 2018; Woodcock et al. 2019). Flower visitation rate was calculated as the number of individual visitors on flowers divided by number of flowers at the plot level over the entire season. We used the additive partitioning of biodiversity effects (Loreau and Hector 2001), an approach that decomposes diversity effects on the basis of proportional deviation from expected values into two components: complementarity effects and selection effects.

The complementarity effect measures the deviation in the average flower visitation rate of ecosystem engineers and associated plant species when blooming alone (i.e., treatments 1 and 2) or in association with each other (i.e., treatment 3). Positive complementarity effects occur with partitioning of flower visitors and indirect facilitation, while negative complementarity effects indicate indirect competition or chemical interference (Loreau and Hector 2001; Barry et al. 2019). The selection effect measures the covariation in the average flower visitation rate of ecosystem engineers and associated plant species between blooming alone (i.e., treatments 1 and 2) and in association (i.e., treatment 3). Positive selection effects occur if species with higher-than-average flower visitation rates are also dominating community-level flower visitation rates in mixtures, and vice versa for negative selection effects.

We considered ecosystem engineers and associated plant species as two different functional groups (i.e., two functional diversity levels) in light of their distinct roles in the ecosystem (Ellison et al. 2005; Schöb et al. 2012; Losapio et al. 2019). We therefore measured the complementarity effect as

$$\mathrm{CE} = 2 \; \overline{\frac{Y_{EE}}{M_{EE}} - 1, \frac{Y_{AP}}{M_{AP}} - 1} \; \overline{M_{EE}, M_{AP}}$$

and the selection effect as

$$SE = 2\ cov\ (\overline{\frac{Y_{EE}}{M_{EE}} - 1,\frac{Y_{AP}}{M_{AP}} - 1,\overline{M_{EE},M_{AP}}})$$

where Y_{EE} and Y_{AP} are flower visitation rates of ecosystem engineers and associated plants when blooming in association (i.e., treatment 3), and M_{EE} and M_{AP} are flower visitation rates of ecosystem engineers and associated plants when blooming separately (i.e., treatments 1 and 2). When flower visitation rate was equal to zero (n = 4), in order to avoid meaningless results (i.e., diversity effects equal to infinite) we considered those infinite values as the maximum diversity effect measured times two (i.e., CE = 0.160 and SE = 0.656; Appendix S1: Table S3). Excluding those data did not change the results. We tested each effect separately with LMs using the measure of diversity effect as response and the engineer species as predictor variables.

Finally, we tested the effects of ecosystem engineers on the proportion of visitor species gained on associated plants in the presence of ecosystem engineers. This measure of species gain was calculated separately for each ecosystem engineer assemblages according to Diamond (1969) as

species gain = appearance$_{engineer\ present}$ / total species

Then, we used an LM with species gain (continuous variable) as a function of ecosystem engineer presence (categorical variable with two levels), ecosystem engineer identity (categorical variable with two levels) and the interaction term between them.

The significance of predictors was tested both in terms of model fit and in terms of explained variance using type-II ANOVA (Fox & Weisberg 2011). Data analysis was conducted in R 3.6.0 (R Core Team 2019) using the packages 'vegan' (Oksanen et al. 2018) for functional diversity, 'picante' (Kembel et al. 2010) for phylogenetic diversity, 'lme4' (Bates et al. 2015) for mixed-effects models, 'car' (Fox and Weisberg 2011) for ANOVA tests and 'emmeans' (Lenth 2019) for least-square means contrasts and Cohen's standardized effect size.

Results

We identified 24 plant species growing within ecosystem engineers and found that both abundance and diversity of plants differed across the three microhabitats overall ($P < 0.001$, Tab. 1). In particular, plant abundance was significantly higher in both engineered microhabitats with *A. tetraquetra* ($P < 0.001$) or *H. spinosa* ($P < 0.001$) than in open microhabitats (Appendix S1: Fig. S2a). Plant diversity was higher with *A. tetraquetra* than without it ($P < 0.001$), while plant diversity was similar with and without *H. spinosa* ($P = 0.159$, Appendix S1: Fig. S2b). Plant

abundance and plant diversity were significantly higher in *A. tetraquetra* than *H. spinosa* ($P <$ 0.001 and $P = 0.037$, respectively).

We identified 75 visitor taxa belonging to 45 families and six orders of insects (Appendix S1: Fig. S1). Among those, the most abundant were *Apis mellifera* (26%), *Megachile parietina* (7%), *Eristalis tenax* (7%), *Scythris iberica* (5%) and *Scaeva albomaculata* (5%). The abundance of flower visitors on associated plant species was significantly different between treatments (i.e., with and without ecosystem engineers) depending on engineer identity ($P < 0.001$, Fig. 2a) and after accounting for the significant effects of flower abundance (Tab. 1). Although associated plants were significantly more visited in the presence than in the absence of ecosystem engineer flowers overall ($P < 0.001$), the effect of *A. tetraquetra* on associated-plant flower visitors was positive ($\hat{C} = 0.74 \pm 0.22$ SE, $P = 0.004$) while the effect of *H. spinosa* was negative ($\hat{C} = 0.71 \pm 0.26$ SE, $P = 0.027$).

Exploring the gain of visitor species on flowers of associated plants in relation to the flowering of ecosystem engineers (Fig. 2b), we found that associated species significantly gained visitor species when growing with *A. tetraquetra* but not with *H. spinosa* ($P < 0.001$ for interaction, Tab. 1). In particular, the number of flower visitors on associated plants increased by *c.* 80% in the presence of *A. tetraquetra* compared with the control ($\hat{C} = 0.27 \pm 0.11$ SE, $P = 0.093$), whereas they doubled on average the number of visitor species in the absence of *H. spinosa* than in its presence ($\hat{C} = -0.29 \pm 0.11$ SE, $P = 0.063$).

After accounting for the effects of plant species richness and flower abundance, we found significant effects of plant removal treatments on visitor phylogenetic diversity ($P = 0.012$, Fig. 3a) that were independent of engineer species identity ($P = 0.233$, Tab. 1). In particular, visitor phylogenetic diversity significantly increased in the presence of both ecosystem engineers and associated plants as compared with associated plants flowering alone ($\hat{C} = 0.94 \pm 0.34$ SE, $P = 0.022$). The contribution of *H. spinosa* was three times as large as that of *A. tetraquetra* ($d = 1.55 \pm 0.49$ and $d = 0.51 \pm 0.50$, respectively). In contrast, visitor phylogenetic diversity did not increase with ecosystem engineers in the presence or absence of associated plants ($\hat{C} = 0.43 \pm 0.41$ SE, $P = 0.546$). Results were consistent across visitor functional groups (Appendix S1: Fig. S3 and Table S4).

Flower visitors belonged to five trophic guilds: pollinators (77% of all taxa), parasitoids (8%), herbivores (7%), predators (4%) and scavengers (4%). Plant removal treatments also influenced visitor functional diversity ($P = 0.017$, Fig. 3b), regardless of engineer identity

(interaction term $P = 0.838$, Tab. 1). When ecosystem engineers and associated plant species were flowering together, the functional diversity of visitors was non-significantly higher than when ecosystem engineers flowered alone ($\hat{C} = 0.15 \pm 0.14$ SE, $P = 0.540$) but 160% higher than when associated plants flowered alone ($\hat{C} = 0.36 \pm 0.13$ SE, $P = 0.018$). Both *A. tetraquetra* and *H. spinosa* positively contributed in a comparable way ($d = 0.95 \pm 0.47$ and $d = 0.99 \pm 0.43$, respectively).

Looking at the effects of plant functional diversity on ecosystem functioning (Fig. 4), we found that complementarity effects of ecosystem engineers and associated plant species on flower visitation rates were positive ($\overline{CE} = 0.043 \pm 0.017$ SE, $P = 0.0131$), whereas selection effects were not significantly different from zero ($\overline{SE} = 0.037 \pm 0.119$ SE, $P = 0.760$). Complementarity and selection effects were both independent of engineer identity ($P = 0.343$ and $P = 0.249$, respectively).

Discussion

Biotic interactions within trophic levels may influence interactions between trophic levels and contribute to strengthening the relationship between biodiversity and ecosystem functions. We provide an experimental framework to test how associations between plants shape plant–visitor interactions, increase visitor diversity at both plant and community level, and support the positive effects of biodiversity on ecosystem functioning and services. Notably, our case-study experiment revealed that complementarity effects of plant functional diversity (i.e., ecosystem engineers and associated plants; Fig. 1) resulted in increased flower visitation rates. These findings suggest that the presence of plant species acting as ecosystem engineers can strengthen the positive contribution of biodiversity to ecosystem functioning. Our research thus helps resolving the overarching question of whether and how facilitation affects BEF relationships, pointing toward a composite impact of both direct and indirect processes.

Plant–plant–insect interactions

Previous studies reported higher diversity of insects in the presence of plant ecosystem engineers than in their absence (Reid & Lortie 2012; Lortie et al. 2016; Ruttan et al. 2016). Recent efforts to address direct biotic interactions across trophic levels at the scale of whole communities indicate that plant–plant facilitation by ecosystem engineers can increase pollinator diversity and support ecological network structure (Losapio et al. 2019). Here, we move beyond this previous

work by addressing not only the occurrence of facilitation by ecosystem engineers of associated plants in terms of increased flower visits, but also evidencing how the presence of ecosystem engineers drives ecosystem functioning via complementarity effects.

We observed idiosyncratic effects of the two engineer species on floral visitation rates and visitor species gain. In fact, plants associated to the ecosystem engineer *A. tetraquetra* gained more flower visitors, most of which belonged to the mutualistic, beneficial guild of pollinators. In contrast, the ecosystem engineer *H. spinosa* decreased the visits to the flowers of associated plants. These results concur with a previous observation that while patches of *A. tetraquetra* and associated plants have positive effects on pollination networks, patches of *H. spinosa* have a negative impact (Losapio et al. 2019). We speculate that the positive, facilitative effects of ecosystem engineers on plant growth and diversity go hand-in-hand with benefits for sexual reproduction in the first case, while facilitation is counterbalanced by competition in the second case. A possible explanation for this result is that *A. tetraquetra* increases visibility of associated plants by harboring them on top of its canopy, while *H. spinosa* restrains visitors to flowers of associated plants that grow underneath its canopy (Losapio et al. 2019).

Since *H. spinosa* was not consistently beneficial to flower visitors of associated plants, yet it had positive overall effects when considered together with *A. tetraquetra*, more thorough investigations are required to test for the mechanistic underpinnings of this context dependency and to determine whether engineers are generally beneficial to the ecosystem. In fact, the increase in functional diversity is not necessarily correlated with increased ecosystem functioning. Increasing the spatial and temporal scales of the study, as well as including other processes such as belowground mutualisms and herbivory could help to resolve some of these inconsistencies and generalize the role of ecosystem engineers.

The idea that plant–plant interactions as well as plant diversity influence interactions between plants and insects is well grounded in the concept of associational effects (Barbosa et al. 2009; Underwood et al. 2014), which states that species interactions involving consumers (e.g., herbivores) and resources (e.g., plants) can be modified by neighbors. For example, a plant can be less vulnerable and suffer less damage when associated with other species than when occurring alone (Underwood et al. 2014). Regarding plant–visitor mutualism, both flower visitation and the reproductive output of a focal plant can be facilitated by diverse coflowering neighboring plant species (Feldman et al. 2004; Ghazoul et al. 2006). The benefits of growing in species-rich communities are associated with different floral displays and rewards (Thomson & Chittka 2001;

Underwood et al. 2014). Here, we found both positive and negative associational effects between plants depending on ecosystem engineer identity, providing new evidence for both pollination facilitation and pollination interference, respectively.

Facilitation and biodiversity–ecosystem functioning

Complementarity among different plant species is one of the key mechanisms by which more diverse plant communities are more productive than monocultures (Hector et al. 1999; Loreau & Hector 2001; Hooper et al. 2005; Tilman et al. 2014; Wright et al. 2017). In addition to increasing productivity, plant richness can also influence the diversity of adjacent trophic levels (Scherber et al. 2010; Blüthgen & Klein 2011; Borer et al. 2012; Ebeling et al. 2018). The positive effects of the association between ecosystem engineers and associated plants propagates through the ecological network, increasing visitor diversity at different trophic levels such as pollinators, parasitoids, predators, scavengers and herbivores. Our results highlight the propagating, cascading effects of biodiversity change that could be linked to facilitation by plants acting as ecosystem engineers. Such positive effects were independent of flower density or plant species richness per se. Furthermore, our findings of higher complementarity effects between plant functional groups confirm our hypothesis that higher flower visitation rates are supported by complementary plant species.

Our results suggest that facilitation-driven plant patches may promote emergent properties that go beyond frequency- or density-dependent mechanisms, and that cannot be deduced by examining single species in isolation from the rest of the community. From our results, it looks like both mechanisms of niche differentiation and flower-visit facilitation are at work. Facilitation between ecosystem engineers and associated plant species may contribute to increase flower attractiveness for shared visitors, meanwhile niche differentiation may widen the resource axis by attracting diverse flower visitors. These types of indirect effects shaping the prevalence of facilitation or competition confirm theoretical predictions and empirical observations on the role of mutualistic networks for species coexistence (Bastolla et al. 2009; Losapio et al. 2019).

Along this line, our study indicates that ecosystem engineers and associated plants can complement each other in attracting visitors. This means that the association between plants with contrasting ecological functions can also attract more flower visitors with different roles than the average expected by the two plant functional groups growing alone. Such plant complementarity is likely due to both the increased attraction of shared pollinators as well as niche differences in

plant–insect interactions. It can be driven by differences in floral traits and preferences and the degree of specialization (Junker et al. 2015; Venjakob et al. 2016; Fornoff et al 2017). Selection effects were absent, indicating that although the engineers *A. tetraquetra* and *H. spinosa* dominate the plant community in terms of abundance (Schöb et al. 2012), they are not dominating the plant community with regard to average attractiveness to flower visitors. A possible mechanism is that visual (e.g., colors) and olfactory (e.g., flower volatiles) cues of neighboring plants can increase the communication display (Junker et al. 2017) in more complex and biodiverse plant communities compared with functionally poor assemblages.

Our study looked at interactions between plants and flower visitors, therefore, overlooking plant organs as leaves and roots, which may give us a more complete picture. Furthermore, we did not directly assess pollen transfer or feeding behavior of flower visitors but deduced their functions from natural history knowledge; this masks potential intra- and inter-specific variability along the mutualistic–antagonistic continuum of flower visitors (Bronstein 2009) and makes it harder to quantify services provided by flower visitors (Winfree et al. 2017). Yet, pollinators showed the most significant changes in abundance among the different treatments (Table S5). In addition, having two engineer species and one set of subordinate plants could make it more difficult to detect selection effects. Finally, we did not completely remove ecosystem engineers but only covered their flowers in order to minimize the impact of our study; so, other facilitative effects associated with microclimate and nutrient conditions were still in place, potentially affecting flower visitors.

The experimental approach we propose here integrates the empirical pairwise design of plant–plant interaction studies with the analytical procedure of partitioning biodiversity effects on ecosystem functioning. By applying it to real world ecosystems, we show how plant facilitation and complementarity can enhance ecosystem functioning across trophic levels. Our experimental design could also be used for testing other hypothesis, including the additivity or synergism of species interactions (Losapio et al. 2019). Despite the limited scale of the case-study experiment, this approach provides a foundation for future studies examining the described phenomena at larger spatial and temporal scales. Indeed, the observed relationships are likely to vary considerably over space and time (Robinson et al. 2018). For this reason, future research should incorporate designs that capture temporal and spatial heterogeneity, including between- and within-year variation as well as differences among individuals and microhabitat conditions. Moreover, since such variation is also scale-dependent, seasonal and yearly network dynamic

should be considered along with local interactions, community-level variation, and changes across the landscape. Future studies should also address mechanisms of visitor behavioral responses to plant–plant networks and expand the network to other organisms and biotic interactions, such as root symbiosis and herbivory. Finally, it will be important to address the consequences of pollinators and other insect guilds for plant fitness, and measuring directly the delivery of ecosystem services.

Conclusions

The proposed experimental framework provides a way to measure how facilitation among plants can scale up to a full network and across seasons and years, ultimately strengthening the contribution of biodiversity to ecosystem functioning via complementarity effects. Our case-study experiment illustrates that complementary effects within a trophic level can increase the diversity and functioning at another trophic level. In synthesis, plant facilitation can support ecosystem functioning both directly via microhabitat amelioration and indirectly via diversity effects. We suggest that facilitation of associated plant species by ecosystem engineers and resulting complementarity for attracting flower visitors are the mechanisms holding together ecological networks. New directions include addressing the temporal variation and spatial heterogeneity of networks, accurately quantifying ecological processes such as pollen transfer, and extending the complexity of the network to multiple interaction types. Revealing the joint role of species interactions and biodiversity within and between trophic levels is needed for understanding the functioning and stability of ecosystems.

results; G.L., R.N., H.B., P.C., C.G., J.P.H., A.M., J.O., A.C.P., P.R., J.S., M.S. and D.S. identified insect species; G.L. analyzed the data with input from J.B., B.S., R.M. and C.S.; G.L. wrote the first draft of the paper and all authors contributed to the subsequent revision. The authors declare no conflict of interest. Animal welfare and endangered species: our research was conducted in accordance with institutional guidelines and in conformance with laws of the Sierra Nevada National Park; the collection of specimens was limited to those necessary for identification.

Supporting Information

Additional supporting information may be found online at: [link to be added in production]

Data Availability

All original data and R code used in this study are publicly available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.dz08kprw0

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Tables

Tab. 1 Summary table of explained variance for the whole model (chi-square and *P*-value) and model fit for single predictor levels (estimate, standard error and *P*-value). Baseline levels: 'open' in Plant abundance and Plant diversity; 'ecosystem engineer' and '*A. tetraquetra*' in Flower visitors; 'engineer & associated' and '*A. tetraquetra*' in functional and phylogenetic diversity of flower visitors; '*A. tetraquetra*' in complementarity and selection effects.

Response and predictor	χ^2	*P*	level	β	SE	*P*
Plant abundance						
Microhabitat	584.4	< 0.001	A. tetraquetra	1.85	0.10	< 0.001
			H. spinosa	0.46	0.12	< 0.001
Plant diversity						
Microhabitat	7.8	< 0.001	A. tetraquetra	0.34	0.09	< 0.001
			H. spinosa	0.12	0.09	0.159
Flower visitors						
Flower abundance	38.4	< 0.001		0.01	< 0.01	< 0.001
Removal treatment	0.7	0.412	Open	-0.74	0.21	< 0.001
Ecosystem eng	2.1	0.146	H. spinosa	-1.10	0.27	< 0.001
Microhabitat : Eco eng	19.9	< 0.001	Open : H.s	1.44	0.32	< 0.001
Visitor phyl diversity						
Plant species richness	0.8	0.367		-0.18	0.20	0.371
Flower abundance	0.2	0.686		< -0.01	< 0.01	0.687
Removal treatment	8.7	0.012	Alone	-0.12	0.51	0.811
			Open	-0.46	0.45	0.313
Ecosystem eng	0.2	0.657	H. spinosa	0.59	0.39	0.138
Removal : Eco eng	2.9	0.233	Alone : H.s	-0.62	0.53	0.251
			Open : H.s	-0.95	0.58	0.109
Visitor fun diversity						
Plant species richness	1.8	0.182		0.09	0.06	0.186
Flower abundance	1.5	0.228		< 0.01	< 0.01	0.232
Removal treatment	8.2	0.017	Alone	-0.20	0.18	0.285
			Open	-0.35	0.17	0.040
Ecosystem eng	0.1	0.857	H. spinosa	-0.04	0.15	0.768
Removal : Eco eng	0.4	0.838	Alone : H.s	0.10	0.21	0.637
			Open : H.s	-0.01	0.20	0.949

Complementarity						
Average	-	-		16.39	6.02	0.011
Ecosystem eng	-	-	H. spinosa	-11.89	8.51	0.174
Selection effect						
Average	-	-		-3.96	2.34	0.103
Ecosystem eng	-	-	H. spinosa	4.31	3.31	0.204
Species gain						
Removal treatment	< 0.1	0.901	Together	0.27	0.11	0.021
Ecosystem eng	0.1	0.716	H. spinosa	0.25	0.11	0.031
Microhabitat : Eco eng	12.2	< 0.001	Together : H.s	-0.56	0.17	< 0.001

Figure legends

Figure 1: (Top) Ecosystem engineers (*Arenaria tetraquetra* on the left, *Hormathophylla spinosa* on the right) with associated plants in Sierra Nevada, Spain. (Bottom) Plant–plant–insect interactions and complementarity. On the left, an ecosystem engineer is visited by three species. On the center, an herb is visited by two species. On the right, when the ecosystem engineer facilitates the growth of the associated herb (blue arrow), the two plants complement each other for flower visitors since both plants are more visited and the community is richer than expected by the average of single plants.

Figure 2: Effects of ecosystem engineers *A. tetraquetra* and *H. spinosa* on the abundance of flower visitors (a) and the proportion of insect species gain (b) for associated plants in the presence vs absence of ecosystem engineers. Shown are marginal means with 95% CI.

Figure 3: Consequences of plant facilitation by ecosystem engineers (effects are marginalized over the two ecosystem engineer species) on the phylogenetic (a) and functional (b) diversity of flower visitors. Shown are marginal means with 95% CI.

Figure 4: Diversity effects of plant–plant facilitation on flower visitation rate. We used additive partitioning of diversity effects (Loreau & Hector 2001), considering ecosystem engineers and associated plants alone as monocultures (i.e. one functional group) and the engineers and associated plants together as a two-functional-group mixture. Flower visitation rate (standardized by flower abundance) was considered as response. Shown are marginal means with 95% CI.
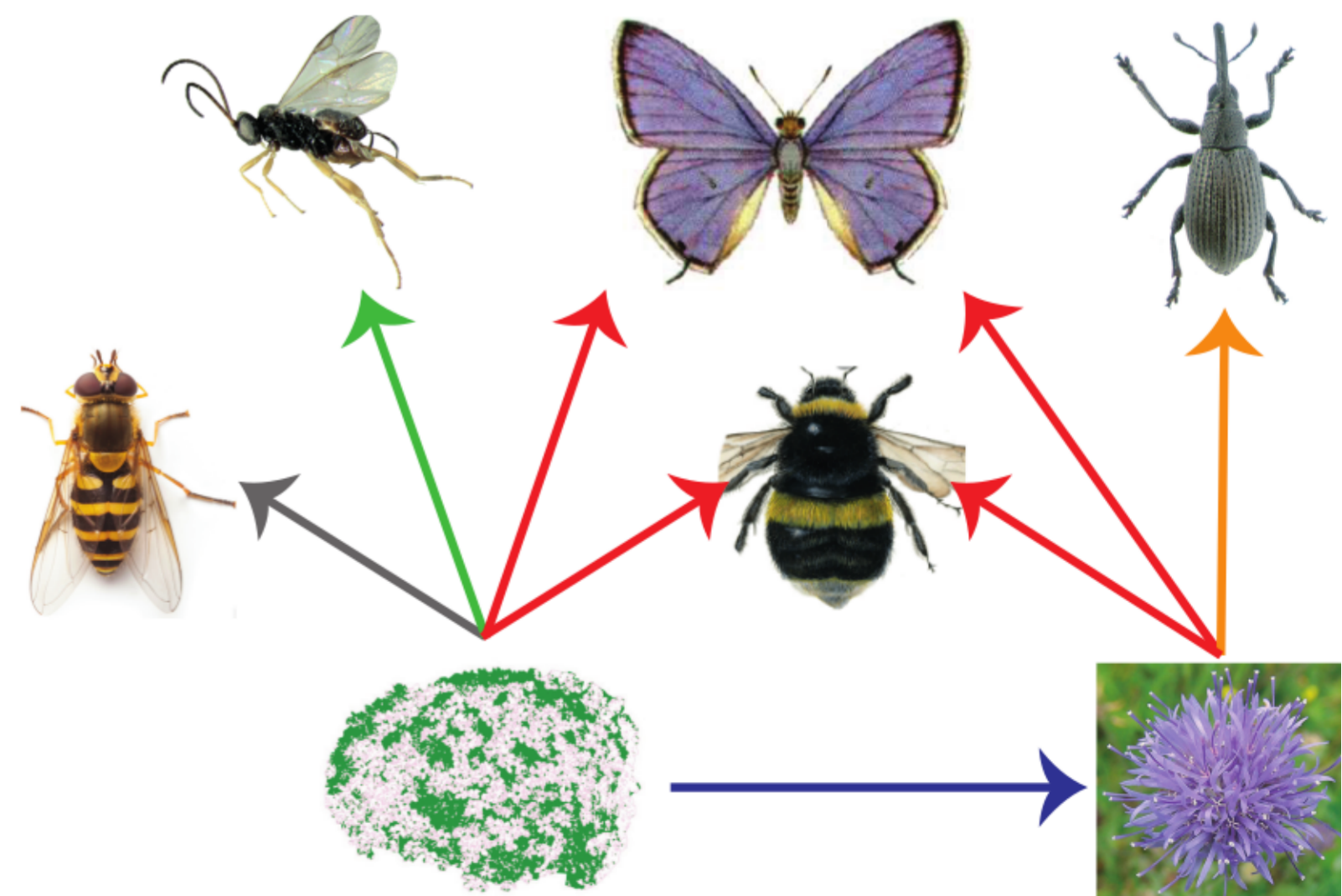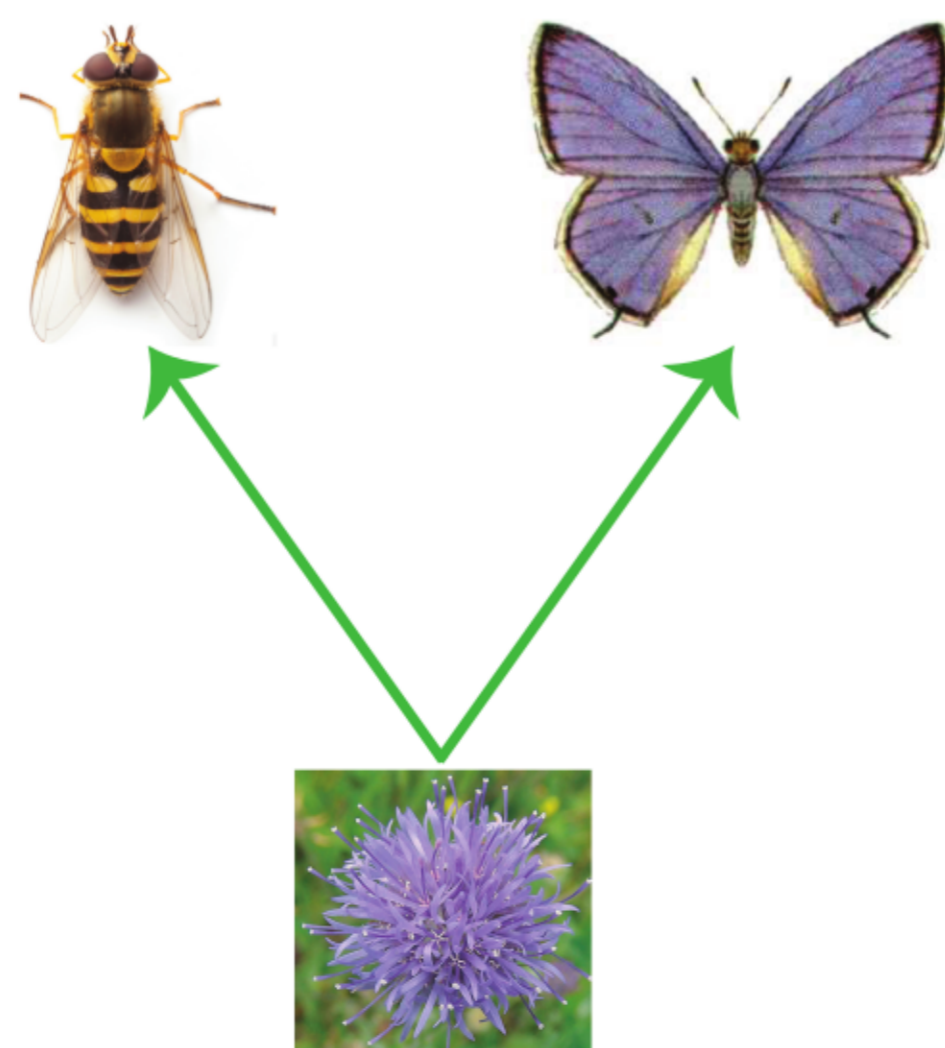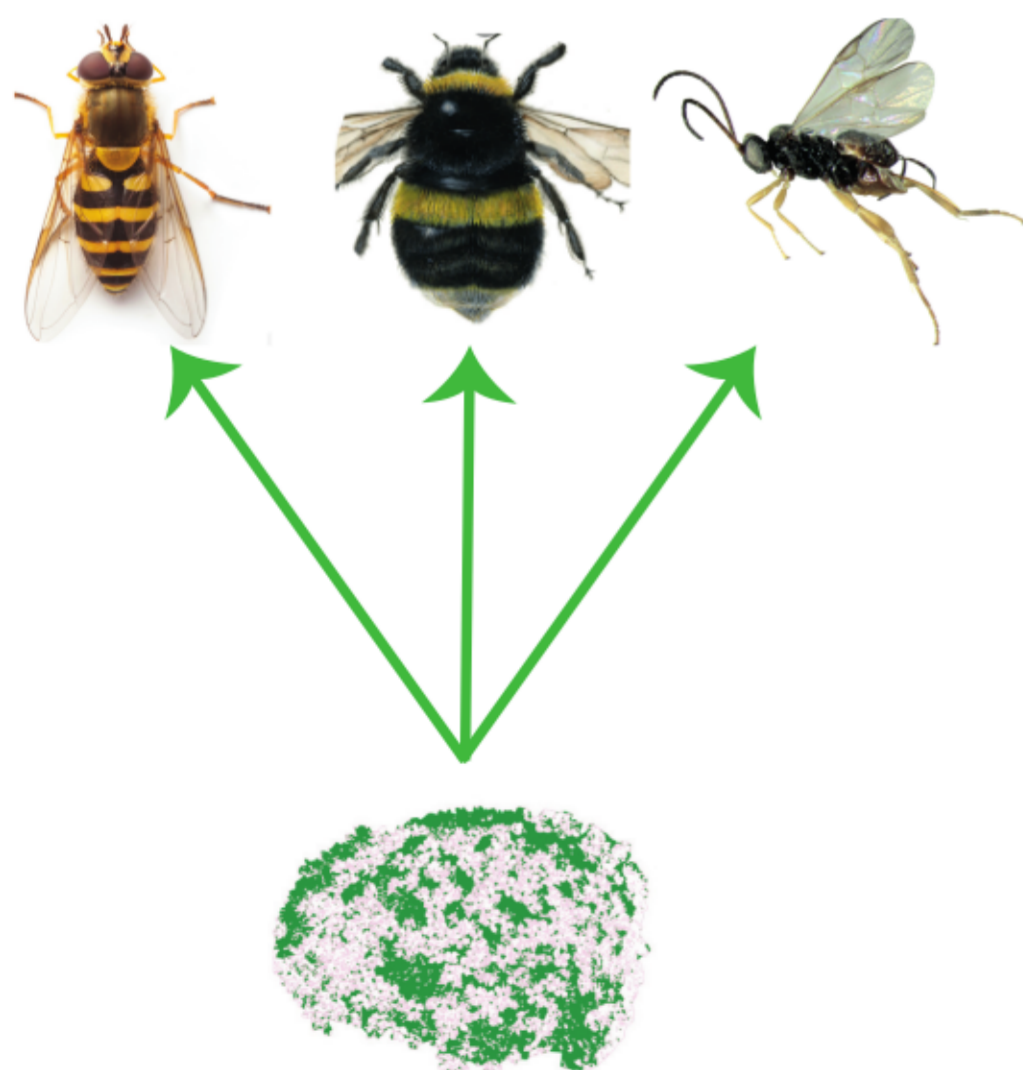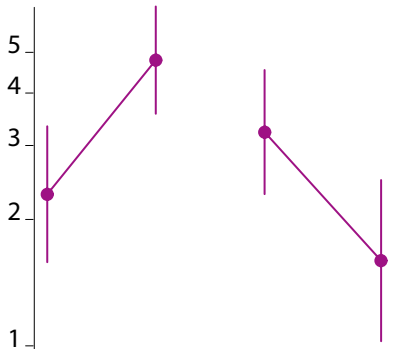
Ecosystem engineer   Associated plant species   Engineer & Associated

(a)

Flower visits

(b)

Visitor species gain

Plants alone
Plants with *A. tetraquetra*
Plants alone
Plants with *H. spinosa*

(a)

Phylogenetic diversity [z-MPD]

(b)

Functional diversity [H]

Engineers alone   Associated alone   Engineers & associated