

Sparse positive and negative weak interactions drive plant species performance in a diverse community

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August 29, 2024

Abstract: 150 words

Main: 4920 words

Number of References: 93

Number of Figures: 5

Number of Tables: 1

Number of Text boxes: 0

Statement of authorship:

Oscar Godoy, Ignasi Bartomeus and Lisa Buche designed the study and collected the data. Margaret Mayfield, Oscar Godoy, Lauren Hallett and Lauren Shoemaker obtained the necessary funding. Lisa Buche analysed the data with substantial input from Oscar Godoy and technical guidance from Peter

Vesk and Christopher Weiss-Lehman. Lisa Buche wrote the manuscript with substantial input from Oscar Godoy and Margaret Mayfield. All co-authors contributed to reviewing the manuscripts.

Data accessibility statement: Data and Code have been deposited on Zenodo, linked to the following Github: <https://github.com/Buchel1984/>; Initial release (V.0). Zenodo. DOI: [10.5281/zenodo.1345994](https://doi.org/10.5281/zenodo.1345994) (version V.1 will be released upon acceptance).

Acknowledgements: We thank a diverse group of people who contributed to field work including María Hurtado, Curro Molina, Sergio Picó and Alvaro Pérez. OG acknowledges financial support provided by the Spanish Ministry of Economy and Competitiveness (MINECO). OG and IB were supported by the European Social Fund through the TASTE project (PID2021- 127607OB-I00). LGS and CWL were supported by NSF, Grant #2019528 and LGS was additionally supported by Wyoming NASA EPSCoR, Grant #80NSSC19M0061. LMH was supported by NSF, Grant #2047239. We thank montesperez.nerea@gmail.com for her illustration in Fig 1.

1 **Abstract**

2 With many species interacting in nature, determining which describe community dynamics is
3 nontrivial. By applying a new Bayesian-sparse modelling approach to an extensive field survey, we
4 assessed the importance of interactions from con- and hetero-specific plants, pollinators, and insect
5 herbivores on plant performance. We compared the inclusion of the interaction effects as aggregate
6 "generic" terms versus specific terms. We found that a continuum of positive to negative interactions,
7 containing mostly generic but a few strong specific interactions, was sufficient to describe variation
8 in plant performance. While interactions with herbivores and conspecifics varied from weakly
9 negative to weakly positive, heterospecific plants mainly promoted competition and pollinators
10 facilitated plants. The consistency of these empirical findings over three years suggests that a broad
11 resolution, including the generic effects of guilds and a few specific groups rather than all pairwise
12 and high-order interactions, can accurately describe species variation in plant performance across
13 natural communities.

14 **1 Introduction**

15 A central aim in ecology is to understand the maintenance of species diversity (Levin, [1970]; Hobbs
16 and Mooney, [1985]). Niche-based explanations for the mechanisms underlying species coexistence
17 rely on the demonstrated importance of biotic interactions for species performance (e.g., growth,
18 fecundity). These effects have been widely studied by combining phenomenological models and
19 experimental manipulations using pairs of competing species within the same trophic guild (Levine
20 and HilleRisLambers, [2009]; Godoy and Levine, [2014]). Yet ecologists rarely quantify these pairwise
21 interaction strengths for whole communities or consider a wider set of interactions within and across
22 trophic guilds simultaneously (García-Callejas et al., [2023]; Chang et al., [2023]; Bimler et al., [2024]).
23 On the contrary, research on food webs and plant-pollinator systems usually examines the structure
24 and complexity of the interaction network without integrating within guild interactions (Godoy et al.,
25 [2018]; Vitali et al., [2023]). As such, it remains untested how the structure of biotic interactions and
26 the relative importance of within- versus across-guild interactions drives species performance and
27 thus the maintenance of local diversity (Vellend, [2010]; Pilosof et al., [2017]).

28 Current phenomenological models of population growth that evaluate coexistence based on
29 an individual performance framework (hereafter called individual performance models) provide
30 context-dependent results. Indeed, they assume that the most expected (not necessarily the most
31 likely in a statistical sense) nature of an interaction between a species pair is the only possible one
32 (Simha, Hoz, and Carley, [2022]). For instance, they assume that plants always compete for resources
33 (Craine and Dybzinski, [2013]; Lanuza, Bartomeus, and Godoy, [2018]; Johnson and Hastings, [2022]),
34 pollinators, based on their mutualistic behaviour, always have positive impacts on plant performance
35 (Vázquez et al., [2015]; Aizen, [2021]), and herbivores act as natural enemies and thus always have
36 negative impacts (Barber et al., [2012]; Aguirrebengoa et al., [2023]). The signs and strengths of

37 interactions between two types of species (or the same type of species) can and do, however, produce
38 different effects as circumstances change. For example, some plants facilitate each other more
39 strongly than they compete for resources (Bimler et al., 2018); some pollinators have negative effects
40 on plants (Magrach et al., 2017); and some herbivores have positive effects on plant performance
41 by promoting further growth (Génin et al., 2021). Such counterexamples are not unusual and
42 their presence in nature begs the question of whether or not we might want to take a more holistic
43 perspective when studying coexistence and the diversity maintenance of real communities—notably
44 one that allows for a continuum of species interactions regardless of trophic guild and type of
45 interaction (Koffel, Daufresne, and Klausmeier, 2021; Gómez, Iriondo, and Torres, 2023; Bimler
46 et al., 2023; Allen-Perkins et al., 2023).

47 In addition to simplifying interaction natures to a single direction, most individual performance
48 models also assume that interactions are all pairwise and direct (Mayfield and Stouffer, 2017).
49 Multispecies interactive effects have, however, been shown to be common and important in many
50 natural systems (Russell and Kaiser-Bunbury, 2019). It remains unclear if ignoring multispecies
51 interactions in individual performance models has minimal effects on model performance or if
52 this omission removes important biological realism. A common way to incorporate multispecies
53 interactions is to allow for higher-order interactions (HOIs), which occur when an interaction
54 between two species is modified by the presence of a third (Billick and Case, 1994; Wootton, 1994).
55 Awareness of the importance of HOIs has increased with growing interest in applying theories
56 designed for pairwise interactions to multispecies natural systems (Levine et al., 2017; Mayfield
57 and Stouffer, 2017; Bimler and Mayfield, 2023; Buche, Bartomeus, and Godoy, 2024). The few
58 empirical studies that have assessed the importance of HOIs in natural systems have occurred for
59 plant-plant interactions (Mayfield and Stouffer, 2017; Lai et al., 2022; Li et al., 2021), microbe
60 interactions (Ishizawa et al., 2024), arthropod interactions (Barbosa, Fernandes, and Morris, 2023)

61 and for one type of interaction between two contrasted guilds - plants and pollinators (Buche,
62 Bartomeus, and Godoy, 2024). These studies all align with theoretical expectations that HOIs
63 are important factors in predicting species' performances (Bairey, Kelsic, and Kishony, 2016;
64 Kleinhesselink et al., 2022; Gibbs, Levin, and Levine, 2022). Despite the literature increasingly
65 supporting the importance of HOIs, most individual performance models omit HOIs, allowing only
66 for direct pairwise interactions (Li et al., 2021).

67 Attempting to include additional complexity in individual performance models yields several
68 well-understood challenges. These models are prone to over-fitting under the classic assumption that
69 each interacting species offers unique insights into the dynamics of a species' performance (Bimler
70 et al., 2023; Terry and Armitage, 2024). However, from the macroevolution literature, we know that
71 closely related species are often more similar than distantly related species (Cavender-Bares et al.,
72 2009) (e.g., compare forbs versus legumes) and that most natural communities exhibit functional
73 redundancy, the phenomenon in which many species have the same ecological role in a given
74 community (Laliberté et al., 2010; Jeliazkov and Chase, 2023). These frameworks suggest that
75 groups of species with similar functional characteristics might interact similarly (Barbier et al., 2018;
76 Barbier, Bunin, and Leibold, 2023) and can be potentially lumped to simplify models; however, how
77 to best group species remains an open question. Traditionally, species have been grouped based
78 on taxonomy or functional groups (Martyn et al., 2020; Uriarte et al., 2004; Straub and Snyder,
79 2006). A more powerful approximation is to use sparse matrix modelling approaches, which allow
80 us to identify which interaction strength and at which grouping level parameters are and are not
81 important for parameterising individual performance models, allowing us to focus only on the
82 unique species interactions that actively affect the performance of a focal species (Hastie, Tibshirani,
83 and Wainwright, 2015; Weiss-Lehman et al., 2022).

84 Here, we examine the degree of complexity in the nature and structure of biotic interactions

necessary to explain the performance of plant species (i.e., seed production, Fig.1.a). Specifically, we test whether the details of within and cross-species interactions are required to explain plant performance in highly diverse communities. We address this question by comparing effects aggregated across species in each trophic guild ('generic terms') with details unique to specific functional or taxonomic groups (family grouping). We coupled data on species abundances and plant performance collected across a three-year period in an annual plant community in southern Europe with a Bayesian sparse modelling approach. This approach explores whether the inclusion of two sources of complexity and four interaction types improves the description of individual performance for four focal annual plant species. The two sources of complexity are the inclusion of higher-order interactions and the variation in sign and strength of net interactions. The four types of interactions considered are: intraspecific plant interactions, interspecific plant-plant, plant-pollinator and plant-herbivore interactions. More specifically, we answered the following questions: (i) Are all pairwise plant-plant, plant-pollinator, and plant-herbivore interactions and their potential 3-way HOIs necessary for describing observational patterns of plant performance? (ii) How do within- and cross-species interactions vary in signs and strengths (from negative to positive and strong to weak)? (iii) Is there consistency in which interactions increase model performance and their nature (sign and strength) across years and/or environments?

102 **2 Methods**

103 **2.1 Natural community**

104 **2.1.1 Study system**

105 Data was collected at the Caracoles Ranch (2680 ha), Doñana National Park, southwest Spain
106 ($37^{\circ}04'001.5'N$, $6^{\circ}19'016.2'W$) between 2019 and 2021 (appendix, fig. S1). The plant communities
107 at Caracoles Ranch are dominated by annual plants from the Poaceae, Asteraceae and Chenopodiaceae
108 families, with almost no perennial species present. The Mediterranean climate has mild winters
109 and an average 20-year annual rainfall of $443 \pm 204\text{mm}$ with high interannual variation (Pesquera,
110 2023) (fig. S3). Soils are sodic saline (electric conductivity $> 4 \text{ dS/m}$ and pH < 8.5). Along ≈ 1
111 km, we set up nine plots that were each divided into 36 subplots of $1m^2$ with aisles of 0.5 m in
112 between (total of 324 subplots). We focus on four consistently abundant focal species for this study:
113 (i) *Leontodon maroccanus* (Asteraceae), LEMA (ii) *Hordeum marinum* (Poaceae), HOMA (iii)
114 *Centaureum tenuiflorum* (Gentianaceae), CETE (iv) *Chamaemelum fuscatum* (Asteraceae), CHFU.

115 **2.1.2 Plant interactions**

116 During the spring growing season of each year, we performed field surveys of annual plant
117 performance in each subplot (appendix, fig. S2–fig. S4). Performance was measured as viable seed
118 production per individual plant (appendix, fig. S6–S5). Together with the estimation of individual
119 performance, we also recorded the number and identity of all local neighbouring plants within a
120 radius of 7.5 cm, including individuals of the same species (appendix, fig. S9). This radius of 7.5 cm
121 is a standard distance used in previous studies of performance in annual plant systems (Levine and
122 HilleRisLambers, 2009; Godoy and Levine, 2014; Godoy et al., 2017; Bimler et al., 2018; Mayfield

123 and Stouffer, 2017). We performed these measurements for one individual per focal species per
124 subplot, unless the species was absent from a given subplot.

125 **2.1.3 Pollinator interactions**

126 To assess interactions between plants and pollinators, we collected data on insect flower visitors
127 (hereafter pollinators) from the onset of the earliest flowers (February) to senescence (June). We
128 recorded the number of floral visits in a plot observed during a 30-minute sampling window each
129 week for a total of 148.5 hours in 2019 and bi-weekly for a total of 54 hours in 2020 and 2021.
130 For example, if a butterfly was present in the plot during our sampling window, we recorded each
131 species of plant it visited in each sub-plot and how many times it touched flowers of the same species
132 (appendix fig S7). We did not measure pollination success, but we restricted our recordings only
133 to pollinators that contacted the plant's reproductive organs (pistil and/or anthers). Additionally,
134 biologically meaningless observations (e.g., bee on a grass individual, or *Coccinella septempunctata*
135 beetles in flower heads) were not included (similar for herbivore observations, described below).

136 **2.1.4 Herbivore interactions**

137 Herbivorous insect data was also collected from the onset of the flowering through senescence
138 (February-June). We recorded the number of herbivores per plant species in each subplot observed
139 in a one-minute sampling window, surveying all plants in each subplot for any herbivorous insect
140 species observed on plant stems, leaves, or flowers and recording plant identity. We sampled each
141 subplot for one minute every week for a total of \approx 76 hours in 2019 and 2021 and 70 hours in 2020
142 (decrease in 2020 due to COVID-19 restrictions; appendix fig S8).

Table 1: Number of potential interactions across the community according to each level of parameter complexity.

level of parameter complexity	grouping	number of potential plant interactions	example of plant	number of potential pollinator interactions	example of pollinator	number of potential herbivore interactions	example of herbivore
high	species	24	<i>Beta macrocarpa</i>	62	<i>Andrena argentata</i>	48	<i>Aiolopus strepens</i>
medium	family	12	Brassicaceae	21	Andrenidae	21	Acridiae
low	functional class	2	forb	4	bee	8	grasshopper

143 2.2 Statistical framework

144 2.2.1 Neighbourhood grouping

145 To compare models with different levels of parameter complexity (Martyn et al., 2020), we fit models
 146 where species within each trophic guild were grouped according to three taxonomic and functional
 147 grouping factors: functional class, family, and species (see tab. I). This allowed us to compare model
 148 performance where interaction strengths were estimated for each species (highest complexity), each
 149 family (medium complexity), or each functional class (lowest complexity), respectively (Tab. I). The
 150 individual performance model described below is applied for each focal species, with each trophic
 151 guild restrained according to one grouping factor.

152 In the main text, we report the results of parameter estimations when the neighbourhood is
 153 grouped according to the taxonomic family. The species and functional group results can be seen in
 154 the appendix. We chose to display the family grouping to show an intermediate level of complexity,
 155 yet our results are consistent across groupings, and none of the grouping levels was consistently
 156 selected as “better” according to the model comparison approach of the “loo” R package version
 157 2.7.0 (appendix A.4.11 tab. S3).

158 **2.2.2 Individual performance model**

159 We quantified the individual performance (i.e., viable seed production) of our four focal plant species
 160 across all three studied years according to a generalisation of the Ricker model (Ricker, [1954]). To
 161 understand how potential complexity changes through time, we fit the below model for each growing
 162 season (t) for each of our focal species. The viable seeds ($F_{i|S,t}$) produced per germinated individual
 163 i interacting with a specified set of neighbours S over the growing season t is described as follow:

$$F_{i|S,t} = \lambda_i e^{D_{i,t}} e^{H_{i,t}} \quad (1)$$

164 where λ_i is the intrinsic performance (i.e., number of seeds) in the absence of interactions (appendix
 165 fig. S18 and eq. S6), D_i represents all pairwise interactions at time t , and H_i represents all HOIs.
 166 All pairwise and HOIs can be either positive or negative. Pairwise and HOIs occur between plants
 167 (denoted “Plt”), herbivores (denoted “Herb”), and pollinators (denoted “Pol”).

168 All potential pairwise interactions are defined as:

$$D_{i,t} = \sum_{j=1}^{Plt} \alpha_{ij,t} N_{j,t} + \sum_{m=1}^{Herb} \alpha_{im,t} N_{m,t} + \sum_{l=1}^{Pol} \alpha_{il,t} N_{l,t} \quad (2)$$

169 where the first sum includes all direct effects of plant species j on focal plant species i . $N_{j,t}$ denotes
 170 the number of neighbours of species j and $\alpha_{ij,t}$ denotes the interaction strength (interspecific
 171 interaction when $j \neq i$ and intraspecific when $j = i$). Similarly, the second term includes all direct
 172 herbivory effects, summed across all herbivores, where $N_{m,t}$ is the average abundance of a herbivore
 173 m on an individual i at time t (i.e., across a growing season). The third term includes pollinator
 174 effects across each pollinator, where $N_{l,t}$ is the average number of visits to a flower of an individual
 175 i from a pollinator l at time t across the growing season. Following García-Callejas et al. (2023) all

176 abundances (i.e., $N_{Plt,t}$, $N_{Herb,t}$, $N_{Pol,t}$) have been rescaled from 0 to 5 to facilitate comparisons
 177 across interaction types by dividing each observation by the maximum abundance observed across
 178 plots for that specific year, multiplied by five.

179 We included HOIs (H_i), which describe the effect of a third group (also called the initiator), which
 180 changes (positively or negatively) the per capita effect (or pairwise interactions) of an interacting
 181 group (also called the transmitter) on a focal species (Li et al., 2021; Woottton, 1994; Kleinhesselink
 182 et al., 2022) (appendix fig. S24). Unlike indirect interaction chains, HOIs are not included in the
 183 pairwise interaction coefficients as they result from both the joint presence of the initiator and the
 184 transmitter densities (e.g., $N_{j,t}$ times $N_{l,t}$). HOIs for a set of neighbours S are defined:

$$H_{i,t} = \sum_{j=1}^{Plt} \sum_{k \neq j}^{Plt} \beta_{ijk,t} N_{j,t} N_{k,t} + \sum_{j=1}^{Plt} \sum_{m=1}^{Herb} \beta_{ijm,t} N_{j,t} N_{m,t} + \sum_{j=1}^{Plt} \sum_{l=1}^{Pol} \beta_{ijl,t} N_{j,t} N_{l,t} \quad (3)$$

185 with $\beta_{ijk,t}$ quantifying how plant species k mediates the effect of species j on focal species i .
 186 Similarly, $\beta_{ijm,t}$ defines the higher-order effect of all herbivores (m in *Herb*) on the nature of a
 187 plant-plant pairwise interaction at time t , and $\beta_{ijl,t}$ for the set of pollinators (l in *Pol*).

188 2.2.3 Bayesian Sparse Modelling Approach

189 We parameterised the above individual performance model from the extensive empirical data set
 190 collected across multiple years using recent statistical advances by Weiss-Lehman et al. (2022),
 191 allowing us to estimate the sign and strength of each relevant interaction across a positive-to-negative
 192 continuum. The Bayesian approach allows within- and cross-trophic guild interactions to be
 193 estimated as continuous probabilities. The sparse approach enables the identification of the relevant
 194 statistical information—in this case, species interactions α and β —needed to accurately describe
 195 neighbourhood effects on performance (fig. 2) (Weiss-Lehman et al., 2022). The Bayesian sparse

196 approach allowed us to parameterise probabilistic sparse matrices, which included four generic
197 interactions (one per trophic guild and intraspecific interaction) and up to 569 potential group-specific
198 interactions (66 pairwise interactions and 503 HOIs, fig. S17).

199 To implement the sparse modelling approach, we first define all pairwise interaction coefficients
200 (e.g., α_{iz} where $z = j \neq i$ for plants, $z = m$ for herbivores, and $z = l$ for pollinators) as linear
201 combinations of aggregated “generic” effects proper to a trophic guild ($\bar{a}_{i,0}$) and effects specific to
202 a taxonomic grouping factor z ($\hat{a}_{i,z}$) such that $\alpha_{iz} = \bar{a}_{i,0} + \hat{a}_{i,z}$. The group-specific terms ($\hat{a}_{i,z}$) are
203 given sparsity-inducing priors in a preliminary model fit, which dynamically shrink all but a subset
204 of these terms to 0, thus identifying any remaining non-zero $\hat{a}_{i,z}$ terms as statistically relevant to
205 focal plant performance (i.e., viable seed production) (Piironen and Vehtari, 2017). The generic
206 effect determines the average strength of species interactions for the taxonomic group, with the $\hat{a}_{i,z}$
207 terms allowing for specific groups to escape this tendency and affect the focal species in non-generic
208 ways (fig. 1b-c-d, generic effect distributions in black and group-specific distributions in red). Note
209 that, as a focal plant always interacts with itself, we did not subject intraspecific effects to the sparsity
210 approach ($\alpha_{ii} = \bar{a}_{ii,t}$) and they were always considered statistically relevant.

211 In contrast, to estimate potential HOIs ($\beta_{ijz,t}$ where j denotes plant species), we assume that not
212 all neighbours have relevant HOIs (Mayfield and Stouffer, 2017; Kleinhesselink et al., 2022). Thus
213 we do not define HOIs with a generic term in our model. Instead, the sparsity-inducing priors are
214 applied directly to each HOI in the preliminary model fit to identify statistically relevant HOIs that
215 deviate from 0 (fig. 2). In other words, for HOIs, we apply the sparse modelling approach to estimate
216 all $\hat{\beta}_{ijz,t}$ (fig. 2; appendix A.4).

217 After the preliminary fit, we performed a final model fit in which the statistically relevant
218 group-specific interaction terms and HOIs were given priors $N(0, 0.1)$ and all non-relevant terms
219 were fixed to 0. In both preliminary and final model fits, the generic terms (e.g., $\bar{a}_{i,0}$) were given

220 priors $N(0, 1)$. Thus, the final model fit allowed us to precisely estimate the statistically relevant
221 terms without the shrinkage imposed by the regularised horseshoe priors (Weiss-Lehman et al.,
222 2022). Finally, we defined intrinsic performance as $\lambda_i = \bar{\lambda}_i U_{i,t}$ where $U_{i,t}$ was the mean fecundity
223 observed for species i at time t and $\bar{\lambda}_i \sim N(0, 1)$ to assure realistic performance estimates (appendix
224 A.4, fig. S19-S20).

225 Thus, the Bayesian sparse approach allows us to fit a highly complex model by dynamically
226 excluding non-relevant group-specific parameters during the preliminary model fit. Indeed fitting a
227 model which included all group-specific parameters with standard priors would not converge without
228 *a priori* simplification (see tab. S2 for convergence and model behaviour). Instead, the Bayesian
229 sparse approach allows such simplification to occur dynamically in response to the information
230 available in the data. As such, the final model fits achieved by the Bayesian sparse approach represent
231 a balance between model complexity (measured by the number of group-specific interaction terms
232 and HOIs included in the final model) and explanatory power (evaluated according to Root mean
233 squared deviance (Thomas, Yen, and Vesk, 2019) and the leave-one-out approximation (Vehtari,
234 Gelman, and Gabry, 2017); Appendix A.4.10; tab. S2, fig. S21b - S22).

235 3 Results

236 We observed that our four focal annual plant species interacted with 24 different species of plants,
237 62 species of pollinators, and 48 species of herbivores (Tab. I). In total, we observed 30,971 plant
238 neighbour individuals, 2,312 individual pollinators and 4,787 herbivores (appendix, fig. S7-S8
239 -S9). Each observation represents one interaction between a focal plant individual and one or more
240 individuals of either a plant (conspecific or heterospecific), a pollinator, or an insect herbivore. We
241 also recorded a broad spectrum of species abundances, with observations of species within a subplot

242 and year ranging from zero to 60 individuals (appendix, fig. S10).

243 For all plants, the Bayesian models achieved a good performance, as indicated by the fact that
244 the models converged well, posterior distributions of parameters were well formed, and explanatory
245 powers were satisfactory according to root mean squared deviance (Thomas, Yen, and Vesk, 2019)
246 and approximations of leave-one-out validation (Vehtari, Gelman, and Gabry, 2017; Weiss-Lehman
247 et al., 2022; appendix A.4.10).

248 **3.1 Model complexity needed to describe natural patterns**

249 We found that generic direct interactions (generic effects that group all species within a trophic
250 guild) were sufficient for describing variation in plant performance. There were only a few groups
251 of interacting species that had specific effects that diverged significantly from trophic guild generic
252 effects (fig. 3 for 2020, and fig. S13 for all years, with the family grouping). These group-
253 specific effects varied between years (see fig. S12 and fig. S14). Specifically, for two of the
254 focal species, *Chamaemelum fuscatum* (CHFU) and *Leontodon maroccanus* (LEMA), two plant
255 families—Asteraceae and Poaceae—directly impacted performance in distinct ways from the generic
256 effects. These non-generic effects arose from the two most common plant families but only for two
257 of our four focal species. The specific effects of the Asteraceae and Poaceae families on the focal
258 species reinforced competition (appendix, tab. S1). Similarly, cross-trophic interactions were well
259 described by the generic effect, with a specific effect appearing only from “beetles” for focal species
260 LEMA in 2020 (see fig. S14). HOIs specific to individual species/families/functional groups were
261 not statistically relevant for any focal species or model.

262 **3.2 Negative and positive interactions are equally prevalent**

263 The likelihood that a given interaction from one of the three trophic guilds was positive or negative
264 varied based on the interaction types (fig. 4 and appendix tab. S1). Interspecific annual plant
265 interactions were dominantly negative (competitive); pollinators had mainly positive impacts on
266 plant performance (minimum of 40.0% of positive effects and up to 100.0%); and intraspecific
267 plant-plant and herbivore impacts were a mix of positive and negative effects. Conspecific effects
268 varied substantially by focal plant species. 90.7% of intraspecific effects for *Centaurium tenuiflorum*
269 (CETE) were positive; while 66.95% were for LEMA, and only about 50% were positive for CHFU
270 and *Hordeum marinum* (HOMA). Similarly, we found that herbivores had negative and positive
271 effects depending on the environmental context, with the smallest percentage of positive effect
272 across any focal species and year of 14.32% (see fig. S15).

273 **3.3 Interaction strength has relatively weak effects on performance**

274 The effect of each trophic guild on plant performance was relatively weak and depended on the
275 interaction type (fig. 5 for family grouping, or fig. S16 for all grouping factors). Heterospecific
276 plant individuals had the most variable effects, with generic effects impacting the performance up to
277 32.4% and group-specific effects up to 43.28% (Poaceae for LEMA in 2019). While most of the
278 estimated effect strengths of pollinators and herbivores were weak (centred around 0), they could
279 increase performance up to 10%, with one particular herbivore functional class, beetles, having a
280 positive effect on LEMA that increased performance by 35.6%. Despite the low strength of most
281 positive effects on performance, in aggregate, they yielded substantial overall impacts. Interestingly,
282 positive interactions are not the by-product of a single highly abundant species (appendix, fig. S10).

283 **4 Discussion**

284 By combining multiple years of extensive field data collection with a new method for estimating
285 the nature and strength of species interactions (Weiss-Lehman et al., 2022), our study quantifies
286 the importance of four common types of ecological interaction (intra- and interspecific plant-plant
287 interactions, plant-pollinator interactions and plant-herbivore interactions) while allowing for higher-
288 order interactions on plant performance. Previous studies either estimated all pairwise interaction
289 strengths (Bimler et al., 2023) or grouped species by functional group or taxonomy, often due to
290 data limitations (Uriarte et al., 2004; Straub and Snyder, 2006; Martyn et al., 2020). Our results
291 suggest an adaptive modelling approach that encompasses both scenarios should be employed. This
292 approach can be applied in highly diverse systems without overfitting the model. Using sparse
293 modelling to include multiple cross-trophic interaction types and higher-order interactions shows
294 that interactions often vary between positive and negative signs. There was little evidence that
295 specific details about HOIs, within or between trophic guilds, add to performance models in our
296 study system.

297 Detailed exploration of generic direct terms points to a more nuanced story. Our findings suggest
298 that though most species within trophic guilds have redundant effects, at least one individual term at
299 the species, family or functional group level emerged as separately important and distinct from the
300 relevant generic term. Such specific individual terms often coincided with keystone or dominant
301 species. Further, while there was strong evidence that the nature of generic pairwise effects varied
302 extensively between positive and negative (fig. 4), most net, abundance-weighted effects were very
303 weak (fig. 5), except for interspecific plant-plant interactions, which tended to be strongly negative
304 (i.e., strongly competitive). Our study clearly shows that most single species within a trophic level
305 do not have important distinct effects on plant performance, but some species do, and these distinct

306 effects are strong and important.

307 The redundancy in statistical estimates of species interaction strengths for most species within
308 trophic guilds was surprising, given the diversity of the functional and evolutionary details in this
309 highly-speciose community. The weak importance of group-specific interactions highlights that
310 the density of neighbours matters more than their identity. For instance, to empirically estimate
311 pollinators' effects on plant performance, the number of total visits is critical; who is doing the
312 visiting might not be so much (Vázquez and Simberloff, 2002). This is because the log-normal
313 distribution of species abundance commonly found in nature (McGill et al., 2007; Cadotte and
314 Tucker, 2017) decreases the detection of group-specific effects over the common effect of a trophic
315 guild (Vázquez and Simberloff, 2002; Lewis et al., 2023). Additionally, the redundant effect of
316 species within trophic guilds on ecological function is commonly found in conservation ecology
317 (Walker, 1992; Naeem, 1998; Biggs et al., 2020). Like the functional redundancy principle, most
318 species might have a generalisable effect on ecological patterns, with a few key species having
319 disproportionate importance.

320 Identifying the key species or taxonomic groups that exhibit a divergent interaction effect from
321 their trophic guild has important ramifications for ecological theory and conservation strategy
322 (Walker, 1992). For instance, we found that grasses, when grouped at the functional level (Grass),
323 family level (Poaceae) or species level (*Hordeum marinum*, HOMA), had an effect that diverged
324 from other heterospecific plants. While plant interactions are dominantly negative, the specific
325 effect from grass individuals reinforced such competition. Similarly, the Asteraceae family, and
326 *Leontodon marocanus*, LEMA in particular, was found to have a specific important effect on
327 (*Hordeum marinum*) in 2020. These two species are the most abundant species in this system,
328 which could explain their strong competitive effect; we speculate this could occur in other grassland
329 ecosystems as the Poaceae and Asteraceae families have distinct ecological strategies leading them

330 to be efficient invaders in many systems around the world (Hallett, Stein, and Suding, 2017; Bowler
331 et al., 2022; Aoyama et al., 2022; Huang et al., 2024). Understanding if these families can coexist
332 with the rest of the plant community despite their strong competitive abilities or are slowly excluding
333 others from the system is critical to predicting the accurate state of the community and potentially
334 managing it.

335 Consistent with their generally strong competitive effect, for the Poaceae family, and specifically
336 *Hordeum marinum*, we found that self-competition rather than other biotic interactions regulate its
337 high abundance. This species is wind-pollinated and generally not very palatable to insects given
338 physical defences (Mcnaughton, 1983). It is also a strongly competitive grass that experiences
339 weak competition from other annual plants. Yet, its consistently strong negative intraspecific effects
340 lead to a reduction of up to 19.2% in its performance relative when grown alone. This finding is
341 consistent with density-dependent self-regulation and thus is a possible explanation for why this
342 species does not come to dominate the system (HOMA, 2020, “Functional” grouping, fig. S15).
343 This finding was only visible because we did not assume a particular interaction direction for each
344 trophic guild.

345 Previous studies investigating species interactions have restrained them to *a priori* directions in
346 their effects (Gómez, Iriondo, and Torres, 2023; Bimler et al., 2023). Allowing for interactions to
347 vary along a continuum of positive-to-negative effects revealed that the effect of pollinators on plants
348 was primarily positive while heterospecific plant-on-plant interactions were mainly competitive,
349 as expected (Ollerton, Winfree, and Tarrant, 2011; Rodger et al., 2021; Adler et al., 2018; Yang
350 et al., 2022); yet, surprisingly, conspecific plants and herbivore interactions with plants were highly
351 variable, including some strong positive effects. Given that we used seed set as our proxy for
352 performance, a positive effect from herbivory may have resulted from the allocation of more energy
353 to seed production due to the stress induced by leaf damaged (Bartomeus, Gagic, and Bommarco,

354 [2015; Aguirrebengoa et al., 2023], or increased growth in compensation for the removal of ageing
355 (or young) tissues. Similarly, the positive effects of some conspecific plants are counter to most
356 theoretical expectations. Still, such positive effects are commonly observed in nature, especially in
357 populations persisting at low densities (aka Allee effect) (Allee and Emerson, 1957; Heyes et al.,
358 2020; Bowler et al., 2022). While positive interactions among individuals of the same species can
359 lead to uncontrolled population growth (Hart, 2023), this positive-feedback loop may be limited
360 by negative effects from individuals of different species (Sheley and James, 2014), the presence
361 of higher trophic levels (Cervantes-Loreto et al., 2021), or temporal variations in the direction of
362 interactions within the same species (Zou, Yan, and Rudolf, 2024), as evidenced in this study.

363 Except for heterospecific plants, the overall net strength of species interactions across trophic
364 levels was weak, suggesting an emerging neutrality in our system. This finding is aligned with
365 classic ecological theory, which posits that the feasibility and stability of ecological systems are
366 promoted by weak species interactions (Gardner and Ashby, 1970; May, 1972; McCann, Hastings,
367 and Huxel, 1998; Allesina and Tang, 2012; Yang et al., 2023). The effect of the heterospecific plants
368 was, however, strong in some instances – showing a potentially strong competition for resources
369 in a system with strong annual climatic variation. The tendency of our system towards neutrality
370 might indicate that other mechanisms beyond density-dependence can play an important role too.
371 These are, for instance, fluctuation-dependent mechanisms such as the spatial and temporal storage
372 effect (Sears and Chesson, 2007; Tan et al., 2017) or relative non-linearity (Hallett et al., 2019)
373 which can drive coexistence between observed species (Johnson and Hastings, 2022). Without
374 further study, however, our results cannot be used to determine which, if either, of these mechanisms,
375 is involved in maintaining the diversity of this system, but targeted experiments to test for these
376 mechanisms are a high priority for future studies.

377 Overall, our findings provide critical empirical evidence on the nature and strength of species

378 interactions in a highly-speciose ecosystem. Our system presents generic weak effects on average
379 rather than being involved in complex sets of pairwise and higher-order interactions. As these
380 effects range from positive to negative interactions they should not be predefined with one specific
381 direction but allowed to vary along a continuum (Koffel, Daufresne, and Klausmeier, 2021; Simha,
382 Hoz, and Carley, 2022; Arroyo-Correa, Jordano, and Bartomeus, 2023). This does not mean we
383 should study complex systems by assuming a random structure of biotic interactions. Instead, we
384 should identify the redundant effects within trophic guilds and the specific interactions that deviate
385 from this redundancy. This can be particularly important for future theoretical work on diversity
386 and conservation strategies for managing strong competitors. Lessons from this study advance our
387 understanding of the structure of biotic interactions under high-dimensional natural systems.

5 Figures

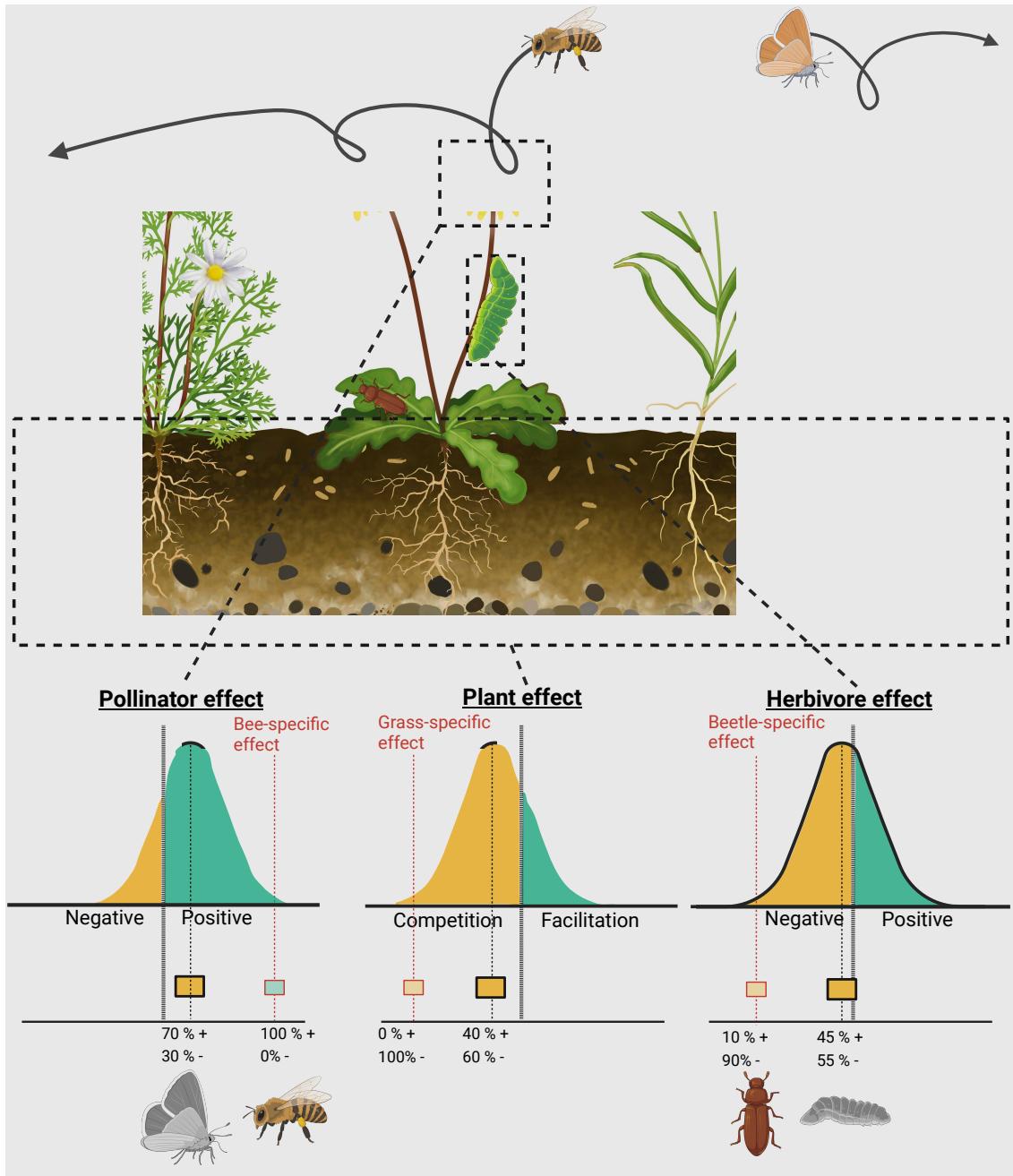


Figure 1: Study system and methodological illustration: Depiction of the four annual plant species studied: *Chamaemelum fuscum* (CHFU), *Leontodon maroccanus* (LEMA), *Hordeum marinum* (HOMA), and *Centaurium tenuiflorum* (CETE), from left to right. We collected data on the number of seeds produced, plant neighbors, herbivores, and pollinators for each focal species. These observations were used to fit an individual performance model to estimate species interactions. The effects could be positive (green) or negative (yellow) based on whether an individual promotes or harms the performance of the focal annual plant.²⁶ Each trophic level (**panel b** for herbivores, **panel c** for heterospecific plants and **panel d** for pollinators) has a generic effect that aggregates across interactions and group-specific deviations from the generic effect (red distribution; represented by coloured species). For example, a "grass-specific effect" could diverge from the generic plant effect. Credit to Nerea Montesperez for the illustration. Extended version in the appendix, fig S11.

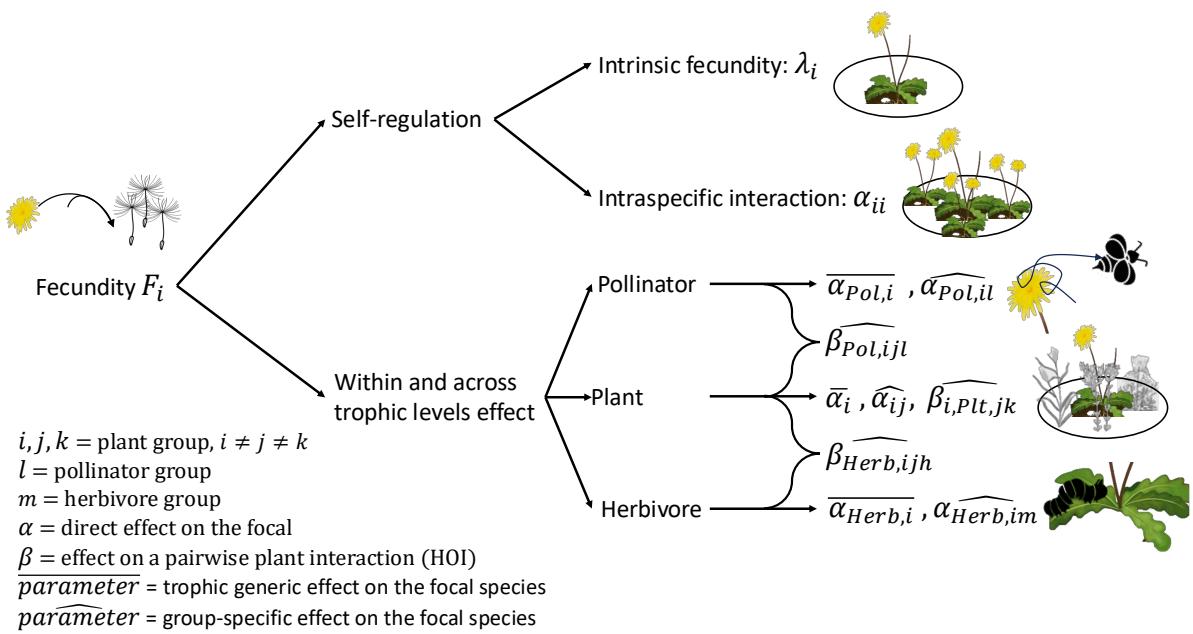


Figure 2: **Depiction of model parameterisation**, relating species performance (number of seeds produced per individual) with self-regulation process and neighbours influence. Self-regulation processes are driven by intrinsic performance and intraspecific interactions. Neighbours affect the focal's performance through plant neighbourhood density and identity, pollinator visitation rate, and herbivore presence, considering both direct effects (α terms) and higher order interactions (β terms).

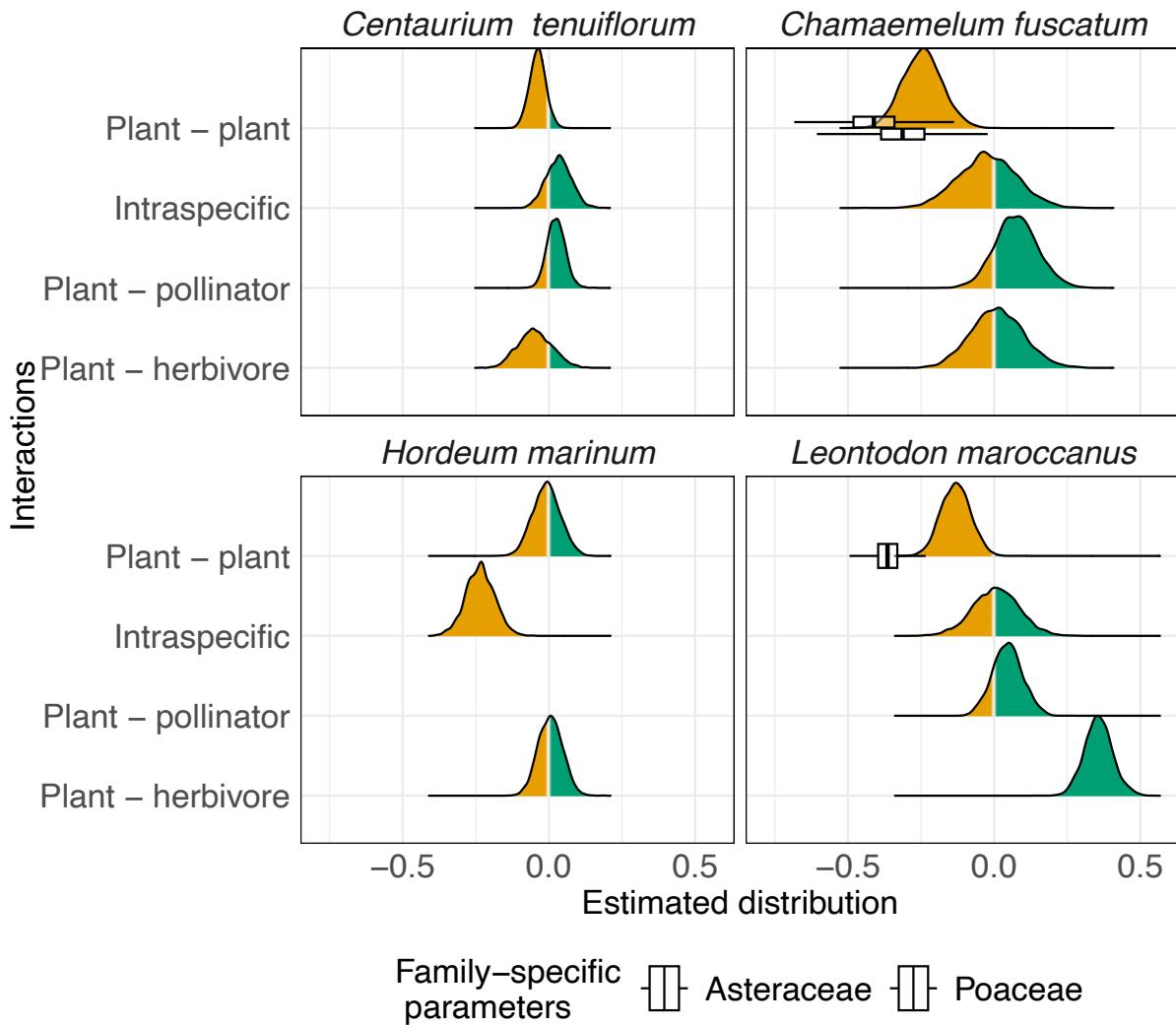


Figure 3: Distribution of generic species interactions and their family-specific interaction, if relevant, for the year 2020. All years and grouping levels in the Appendix. Fig S12

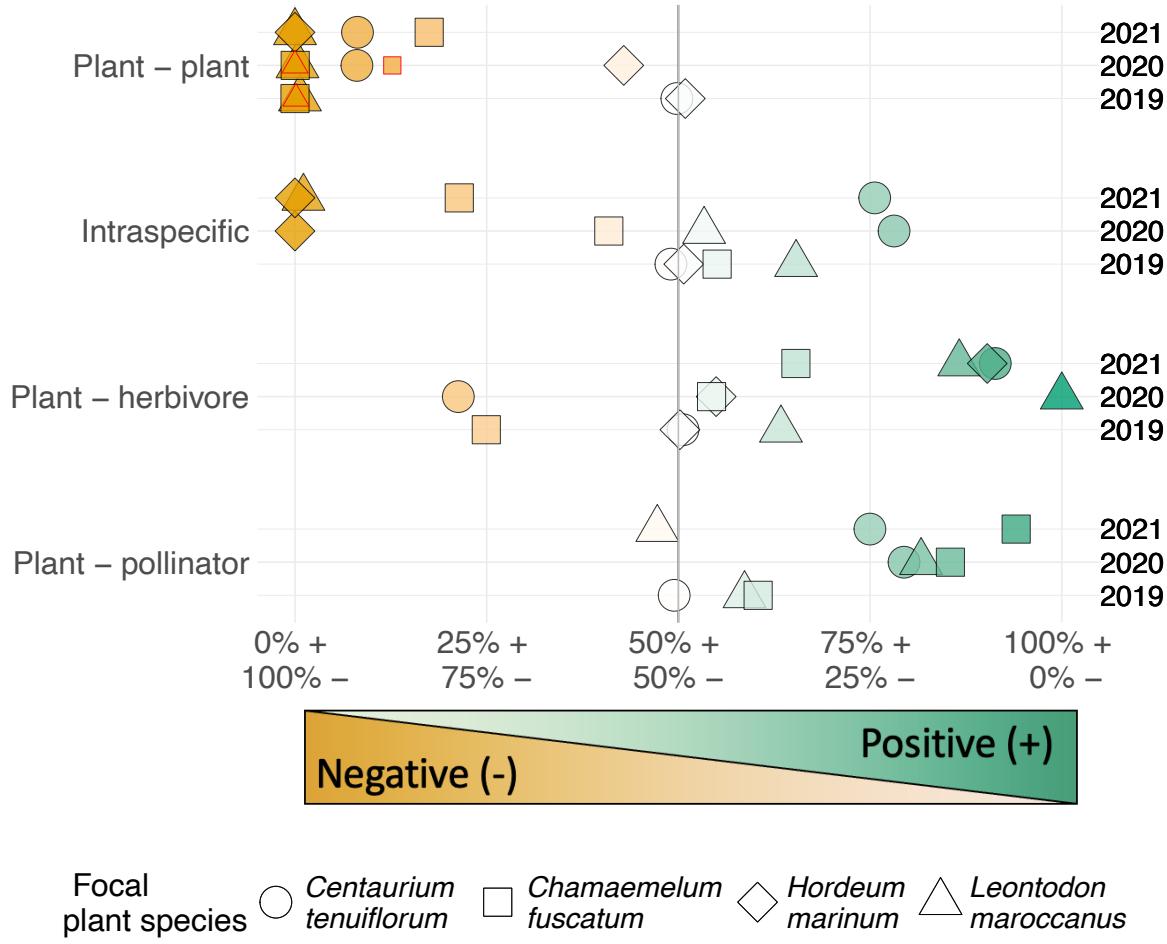


Figure 4: Percentage of positive vs negative distributions of effects depends on the focal species and trophic level. Each interaction is situated on the spectrum, from purely positive (LEMA, plant - pollinators, 2021) to purely negative (HOMA, plant - plant, 2021) or neutral (CHFU, plant-herbivore, 2020). Pollinators have nearly all positive effects on plant species. Conversely, plant neighbors produced mainly competitive interactions. Plant family-specific interactions (circled in red) are always strongly competitive when present (e.g., LEMA and CHFU). Overall, interactions vary across the continuum depending on the annual condition, focal species, and trophic level. The points encircled in red are family-specific interactions acting on the generic interaction designated by their filling. Results depict species grouped by taxonomic family. All grouping levels in the Appendix Fig S15

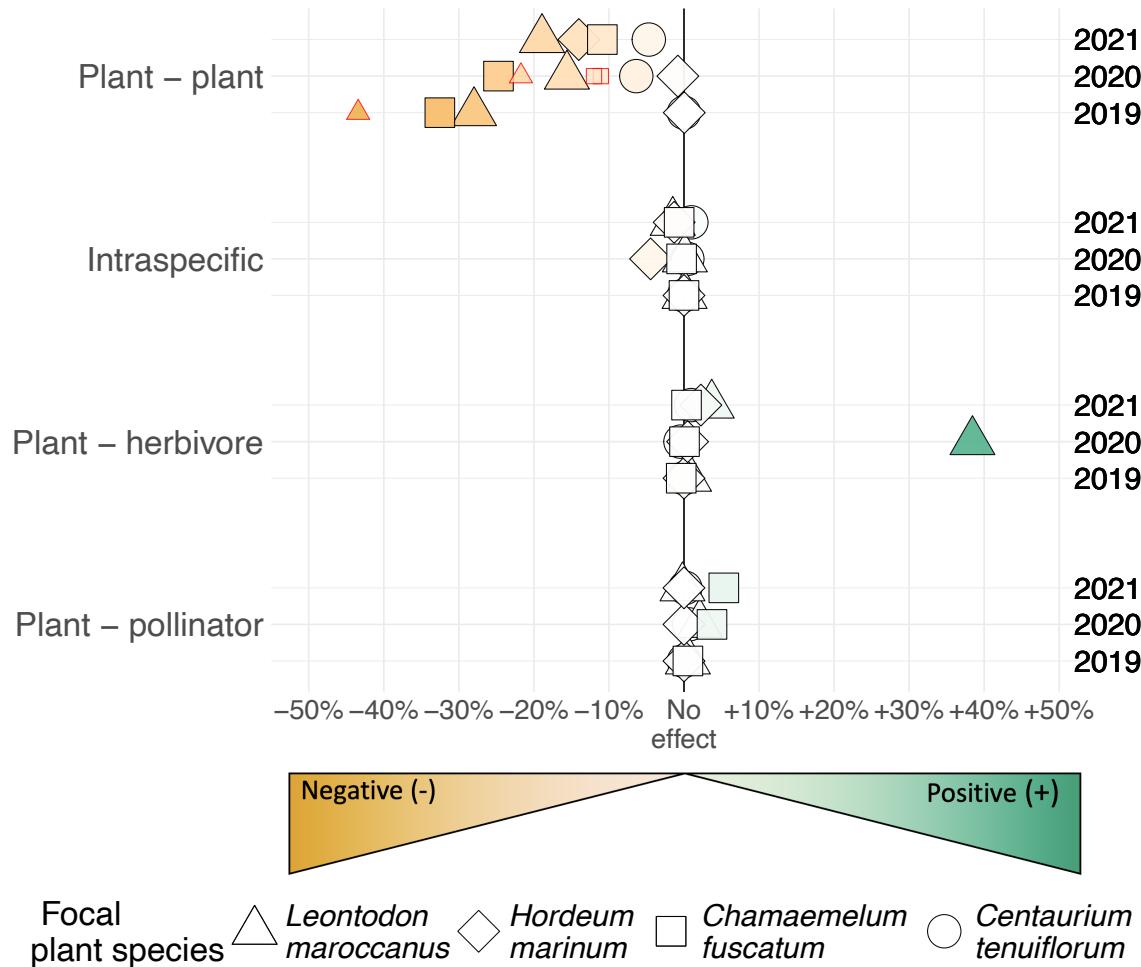


Figure 5: Realised averaged effect of species interaction on individual performance in percentages (%), weighted by the mean number of individuals observed in each trophic level. The strength and direction of species interaction depend on the focal species and trophic level. The effects are overall small and centred around 0, with neutral on performance. Yet, heterospecific plant individuals strongly reduce performance, and pollinators mainly increase performance. The points encircled in red are family-specific interactions acting on the generic interaction designated by their filling. Results depict species grouped by taxonomic family. All grouping levels in the Appendix Fig S16

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