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A Continuum From Positive to Negative Interactions Drives Plant Species' Performance in a Diverse Community

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ABSTRACT

With many species interacting in nature, determining which interactions describe community dynamics is nontrivial. By applying a computational modeling approach to an extensive field survey, we assessed the importance of interactions from plants (both inter- and intra-specific), pollinators and insect herbivores on plant performance (i.e., viable seed production). We compared the inclusion of interaction effects as aggregate guild-level terms versus terms specific to taxonomic groups. We found that a continuum from positive to negative interactions, containing mostly guild-level effects and a few strong taxonomic-specific effects, was sufficient to describe plant performance. While interactions with herbivores and intraspecific plants varied from weakly negative to weakly positive, heterospecific plants mainly promoted competition and pollinators facilitated plants. The consistency of these empirical findings over 3 years suggests that including the guild-level effects and a few taxonomic-specific groups rather than all pairwise and high-order interactions, can be sufficient for accurately describing species variation in plant performance across natural communities.

1 | Introduction

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

Margaret Mayfield and Oscar Godoy have contributed equally to this work.

Bimler and Mayfield phenomenological models of population growth that evaluate coexistence based on an individual performance framework (hereafter called individual performance models) provide context-dependent results. Indeed, they assume that the most expected (not necessarily the most likely in a statistical sense) nature of an interaction between a species pair is the only possible one (Simha et al. 2022). For instance, first, they assume that plants always compete for resources (Craine and Dybzinski 2013; Lanuza, Bartomeus and Godoy, 2018; Johnson and Hastings 2022). Second, based on their mutualistic behavior, pollinators always have positive impacts on plant performance (Vázquez et al. 2015; Aizen 2021). Finally, herbivores act as natural enemies and thus always have negative impacts (Barber et al. 2012; Aguirrebengoa et al. 2023). The signs and strengths of interactions between two types of species (or the same type of species) can and do, however, produce different effects as circumstances change. For example, some plants facilitate each other more strongly than they compete for resources (Bimler et al. 2018); some pollinators have negative effects on plants (Magrach et al. 2017); and some herbivores have positive effects on plant performance by promoting further growth (Génin et al. 2021). Such counterexamples are not unusual and their presence in nature begs the question of whether or not we might want to take a more holistic perspective when studying coexistence and the diversity maintenance of real communities—notably one that allows for a continuum of negative and positive species interactions regardless of trophic guild and type of interaction (Koffel, Daufresne, and Klausmeier 2021; Gómez, Iriondo, and Torres 2023; Bimler et al. 2023; Allen-Perkins et al. 2023).

In addition to simplifying interactions to a single nature (sign), most individual performance models also assume that interactions are all pairwise and direct (Mayfield and Stouffer 2017). Multispecies interactive effects have, however, been shown to be common and important in many natural systems (Bimler and Mayfield 2023). It remains unclear if ignoring multispecies interactions in individual performance models has minimal effects on model performance or if this omission removes important biological realism. A common way to incorporate multispecies interactions is to allow for higher-order interactions (HOIs), which occur when an interaction between two species is modified by the presence of a third (Li et al. 2021). Awareness of the importance of HOIs has increased with growing interest in applying theories designed for pairwise interactions to multispecies natural systems (Levine et al. 2017; Mayfield and Stouffer 2017; Bimler and Mayfield 2023; Buche, Bartomeus, and Godoy 2024). The few empirical studies that have assessed the importance of HOIs in natural systems have occurred for plant–plant interactions (Mayfield and Stouffer 2017; Lai et al. 2022; Li et al. 2021), microbe interactions (Ishizawa et al. 2024), arthropod interactions (Barbosa, Fernandes, and Morris 2023) and for one type of interaction between two contrasted guilds—plants and pollinators (Buche, Bartomeus, and Godoy 2024). These studies all align with theoretical expectations that HOIs are important factors in predicting species' performances (Bairey, Kelsic, and Kishony 2016; Kleinhesselink et al. 2022; Gibbs, Levin, and Levine 2022). Despite the literature increasingly supporting the importance of HOIs, most individual performance models omit HOIs, allowing only for direct pairwise interactions (Li et al. 2021).

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

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, Figure 1a). Specifically, we test whether the details of within and cross-species interactions are required to explain plant performance in a highly diverse community. We address this question by comparing effects aggregated across species in each trophic guild ('guild-level terms') with details unique to specific functional or taxonomic groups (e.g., family grouping). We coupled data on species abundances and plant performance collected across 3 years in an annual plant community in southern Europe with a Bayesian sparse matrix modeling approach. This approach explores whether the inclusion of four interaction types and two sources of complexity improves the description of individual performance for four focal annual plant species. The four types of direct interactions considered mirror the trophic guilds present in the system: intraspecific plant interactions, interspecific plant–plant, plant–pollinator and plant–herbivore interactions. The two sources of complexity are the inclusion of higher-order interactions and the variation in sign and strength of net interactions. Examining patterns in interactions' nature, we answered the following questions: (i) Are all pairwise plant–plant, plant–pollinator and plant–herbivore interactions and their potential three-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?

2 | Methods

2.1 | Natural Community

2.1.1 | Study System

Data was collected at the Caracoles Ranch (2680 ha), Doñana National Park, southwest Spain (37°04001.5'N, 6°19016.2′W)

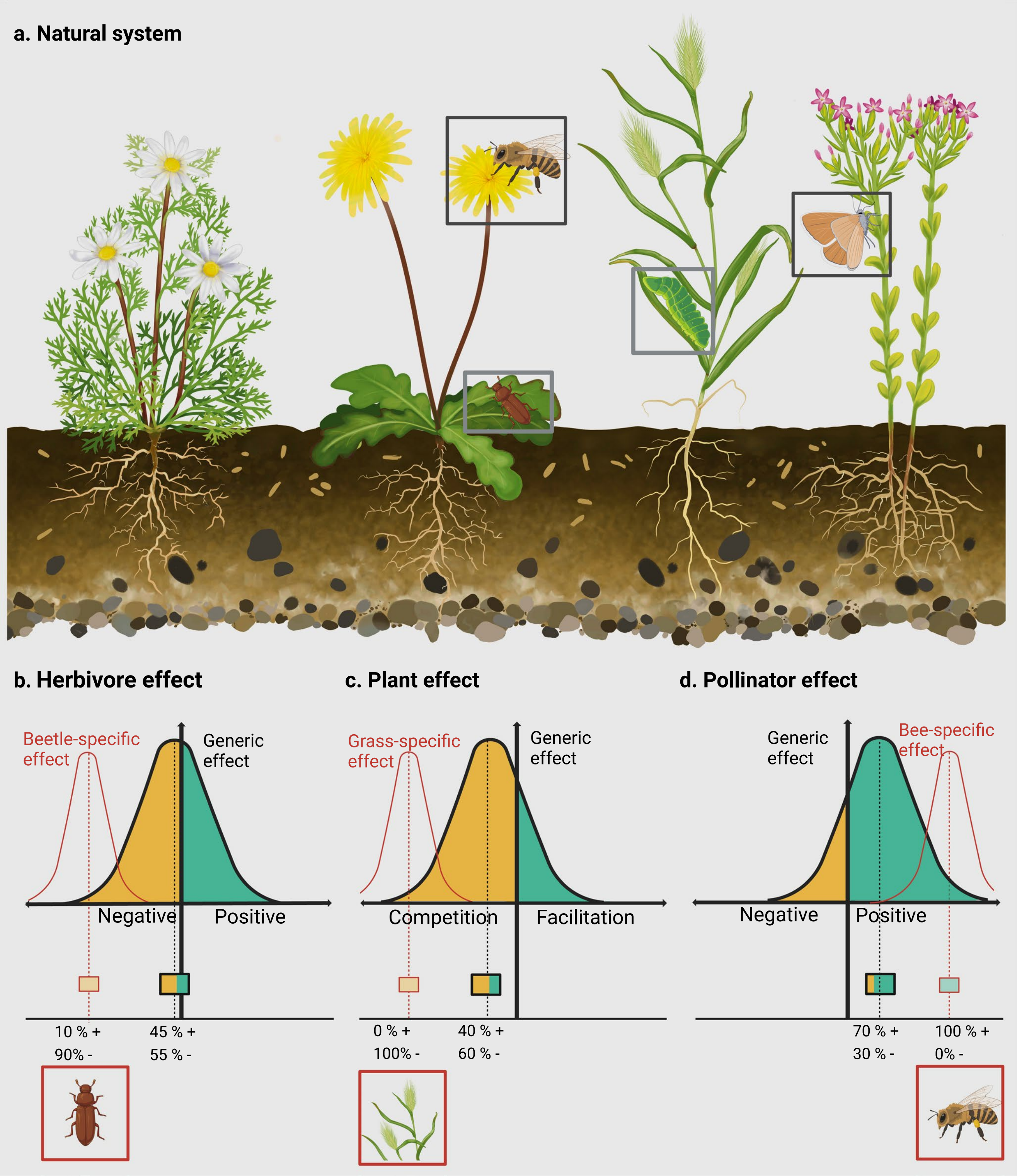

FIGURE 1 | Study system and methodological illustration: Depiction of the four annual plant species studied: *Chamaemelum fuscatum* (CHFU), *Leontodon maroccanus* (LEMA), *Hordeum marinum* (HOMA) and *Centaurium tenuiflorum* (CETE), from left to right. We collected data on the number of seeds produced, plant neighbors, herbivores and pollinators for each focal species (panel a). 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. Each trophic level (panel b for herbivores, panel c for interspecific plants and panel d for pollinators) has a guild-level effect that aggregates across interactions and taxonomic-specific deviations from the guild-level effect (red distribution; represented by colored species). For example, a 'grass-specific effect' could diverge from the plant-level effect. Credit to Nerea Montesperez for the illustration and Biorender. Extended version is shown in Figure S12.

between 2019 and 2021 (Figure S1). The plant communities at Caracoles Ranch are dominated by annual plants from the Poaceae, Asteraceae and Chenopodiaceae families, with almost no perennial species present. The Mediterranean climate has mild winters and an average 20-year annual rainfall of 443 ± 204 mm with high interannual variation (Pesquera 2023) (Figure S3). Soils are sodic saline (electric conductivity > 4 dS/m and pH < 8.5). Along ≈1 km, we set up nine plots that were each divided into 36 subplots of 1 m^2 with aisles of 0.5 m in between (total of 324 subplots). We focus on four consistently abundant focal species for this study:

(i) *Leontodon maroccanus* (Asteraceae), LEMA (ii) *Hordeum marinum* (Poaceae), HOMA (iii) *Centaurium tenuiflorum* (Gentianaceae), CETE (iv) *Chamaemelum fuscatum* (Asteraceae), CHFU.

2.1.2 | Plant Interactions

During the spring growing season of each year, we performed field surveys of annual plant performance in each subplot (Figures S2–S4). Performance was measured as viable seed production per individual plant, with viability assessed by manually counting all seeds with inflated bodies and light color (Figures S5,S6). Together with the estimation of individual performance, we also recorded the number and identity of all local neighboring plants within a radius of 7.5 cm (e.g., Godoy and Levine (2014) and Bimler et al. (2018)), including individuals of the same species (Figure S10). We performed these measurements for one individual per focal species per subplot, unless the species was absent from a given subplot.

2.1.3 | Pollinator Interactions

To assess interactions between plants and pollinators, we collected data on insect flower visitors (hereafter pollinators) from the onset of the earliest flowers (February) to senescence (June) in each subplot. We recorded the number of floral visits observed during a 30-min sampling window each week for a total of 148.5 h in 2019 and bi-weekly for a total of 54 h in 2020 and 2021. For example, if a butterfly was present in the plot during our sampling window, we recorded each species of plant it visited in each sub-plot and how many times it touched flowers of the same species (Figure S7). We did not measure pollination success, but we restricted our recordings only to pollinators that contacted the plant's reproductive organs (pistil and/or anthers).

2.1.4 | Herbivore Interactions

Herbivorous insect data was collected during the same months (February–June). We recorded the number of herbivores per plant species in each subplot observed in a 1-minute sampling window, surveying all plants in each subplot for any herbivorous insect species observed on plant stems, leaves, or flowers and recording plant identity. We sampled each subplot for 1 minute every week for a total of about 76 h in 2019 and 2021 and 70 h in 2020 (decrease in 2020 due to COVID-19 restrictions; Figure S8).

2.2 | Statistical Framework

2.2.1 | Neighbourhood Grouping

To compare models with different levels of parameter complexity (Martyn et al. 2020), we fit models where species within each trophic guild were grouped according to three taxonomic and functional grouping factors: functional group, family, and species (Table S1). This combination of grouping factors reflects species' ecology and phylogeny, while balancing ease of implementation, but alternative grouping could have been done according to functional traits or based on a cluster analysis (Laliberte et al. 2010; Jeliazkov and Chase 2023). The taxonomic grouping allowed us to compare model performance where taxonomic-specific interaction could be detected for each species (highest complexity), each family (medium complexity), or each functional class (lowest complexity), respectively. The individual performance model described below is applied for each focal species, with each trophic guild restrained according to a grouping factor.

In the main text, we report the results of parameter estimations when the neighborhoods are each functional group. The species and family results can be seen in the appendix. We chose to display the functional grouping to show the level of complexity with the highest number of specific interactions detected. Yet, our results are consistent across groupings, and none of the grouping levels was consistently selected as 'better' according to the model comparison approach of the 'loo' R package version 2.7.0 (Appendix S4.11: Table S10).

2.2.2 | Individual Performance Model

We quantified variation in individual performance of our four focal plant species across all three studied years according to a generaliation of the Ricker model (Ricker 1954). To understand how potential complexity changes through time, we fit the below model for each growing season (t) for each focal species. The viable seeds ($F_{i,t}$) produced per germinated individual i over the growing season t is described as follow:

$$F_{i,t} = \lambda_i e^{D_{i,t}} e^{H_{i,t}} \tag{1}$$

where λ_i is the intrinsic performance (i.e., number of seeds) in the absence of interactions (Figure S19 and equation S6), $D_{i,t}$ represents all pairwise interactions at time t and $H_{i,t}$ represents all HOIs. All pairwise and HOIs can be either positive or negative. Pairwise and HOIs occur between plants (denoted 'Plt'), herbivores (denoted 'Herb') and pollinators (denoted 'Pol'). Note that we did not include a spatial parameter as the residuals at the subplot level showed consistently low levels of spatial autocorrelation (Table S5).

All potential pairwise interactions are defined as:

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

where the first sum includes all direct effects of plant species j on focal plant species i. $N_{j,t}$ denotes the number of neighbours of species j and $\alpha_{ij,t}$ denotes the interaction strength (interspecific interaction when $j \neq i$ and intraspecific when $j = i$). Similarly, the second term includes all direct herbivory effects, summed across all herbivores, where $N_{m,t}$ is the average abundance of a herbivore.

m on an individual i at time t (i.e., across a growing season). The third term includes pollinator effects across each pollinator, where $N_{l,t}$ is the average number of visits to a flower of an individual i from a pollinator l across the growing season t. Following García-Callejas et al. (2023), all abundances (i.e., $N_{Plt,t}$, $N_{Herb,t}$, $N_{Pol,t}$) have been rescaled from 0 to 5 to facilitate comparisons across interaction types by dividing each observation by the maximum abundance observed across plots for that specific year, multiplied by five.

We included HOIs, which describe the effect of a third group (initiator), which changes the per capita effect of an interacting group (transmitter) on a focal species (Li et al. 2021). Unlike indirect interaction chains, HOIs are not included in the pairwise interaction coefficients as they result from both the joint presence of the initiator and the transmitter densities (e.g., $N_{j,t}$times $N_{l,t}$). HOIs for a set of neighbors are defined as:

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

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

2.2.3 | Bayesian Sparse Matrix Modelling Approach

We parameterized the above individual performance model from the extensive empirical data set collected across multiple years using recent statistical advances by Weiss-Lehman et al. (2022), allowing us to estimate the sign and strength of each relevant interaction across a positive-to-negative continuum. The Bayesian approach allows within- and cross-trophic guild interactions to be estimated as continuous probabilities. The sparse matrix approach enables the identification of the relevant statistical information—in this case, species interactions α and β—needed to accurately describe neighborhood effects on performance (Figure S18) (Weiss-Lehman et al. 2022).

To implement the sparse modeling approach, we first define all pairwise interaction coefficients (e.g., α_{iz} where $z = j \neq i$ for plants, $z = m$ for herbivores and $z = l$ for pollinators) as linear combinations of aggregated guild-level effects proper to a trophic guild ($\overline{a}_{i,0}$) and effects specific to a taxonomic grouping factor z such that $\alpha_{iz} = \overline{a}_{i,0} + \widehat{a}_{i,z}$. The taxonomic-specific terms ($\widehat{a}_{i,z}$) are given sparsity-inducing priors in a preliminary model fit, which dynamically shrink all but a subset of these terms to 0, thus identifying any remaining non-zero $\widehat{a}_{i,z}$ terms as statistically relevant to focal plant performance (Piironen and Vehtari 2017). The guild-level effect determines the average strength of species interactions for the guild, with the $\widehat{a}_{i,z}$ terms allowing for specific taxonomic groups to escape this tendency and affect the focal species in non-generic ways (Figure 1b–d). Note that, as a focal plant always interacts with itself, we did not subject intraspecific effects to the sparse matrix approach ($\alpha_{ii} = \overline{a}_{ii,t}$)and they were always considered statistically relevant.

In contrast, to estimate potential HOIs ($\beta_{ijz,t}$ where j denotes a plant species), we assume that not all neighbors have relevant HOIs (Mayfield and Stouffer 2017; Kleinhesselink et al. 2022). Thus HOIs are not defined with a guild-level term in our model. Instead, the sparsity-inducing priors are applied directly to each HOI in the preliminary model fit to identify statistically relevant HOIs ($\widehat{\beta}_{ijz,t}$) that deviate from 0 (Figure S18, Appendix S4).

After the preliminary fit, we performed a final model fit in which the statistically relevant taxonomic-specific terms and HOIs were given priors $N(0,0.1)$ and all non-relevant terms were fixed to 0. In both preliminary and final model fits, the guild-level terms (e.g., $\overline{a}_{i,0}$) were given priors $N(0,0.1)$ (Appendix S4, Figures S20,S21). The final model fit allowed us to accurately estimate the statistically relevant terms without the shrinkage imposed by the regularised horseshoe priors (Weiss-Lehman et al. 2022). Finally, we defined intrinsic performance as $\lambda_i = \overline{\lambda_i} U_{i,t}$ where $U_{i,t}$ was the mean fecundity observed for species i at time t and $\overline{\lambda_i} \sim N(0,1)$ to assure realistic performance estimates.

Thus, the Bayesian sparse matrix approach allows us to fit a highly complex model by dynamically excluding non-relevant taxonomic-specific parameters during the preliminary model fit. Indeed, fitting a model that included all taxonomic-specific parameters (up to 62 pairwise interactions and 577 HOIs, Table S6) with standard priors would not converge without a priori simplification (see Table S9 for convergence and model behavior). The Bayesian sparse matrix approach allows such simplification to occur dynamically in response to the information available in the data. As such, the final model fits represent a balance between model complexity (measured by the number of taxonomic-specific terms and HOIs included in the final model) and explanatory power (evaluated according to root mean squared deviance (Thomas et al. 2019) and the leave-one-out approximation (Vehtari et al. 2017); Appendix S4.10: Table S9, Figures S22b,S23).

3 | Results

We observed that our four focal annual plant species interacted with 24 different species of plants, 48 species of pollinators, and 15 species of herbivores (Table S1). In total, we observed 30,971 plant neighbor individuals, 2312 individual pollinators and 4787 herbivores (Figures S7–S10). Each observation represents one interaction between a focal plant individual and one or more individuals of either a plant (intraspecific or interspecific), a pollinator or an insect herbivore. We also recorded a broad spectrum of species abundances, with observations of species presence within a subplot and year ranging from one to 60 individuals (Figure S11).

For all plants, the models achieved good performance, as indicated by the fact that the models converged well, posterior distributions of parameters were well formed, and explanatory powers were satisfactory according to root mean squared deviance and approximations of leave-one-out validation (Appendix S4.10).

3.1 | Model Complexity Needed to Describe Natural Patterns

We found that guild-level pairwise interactions were sufficient for describing variation in plant performance. There were only a few taxonomic groups that had specific effects that diverged significantly from guild-level effects (Figure 2 for 2020, and Figures S13–S15 for all years and grouping).

These taxonomic-specific effects varied between years (Figure 2). Specifically, for one of the focal species, *Leontodon maroccanus* (LEMA), one plant functional group, 'Grass' directly impacted performance in distinct ways from the guild-level effects (Figure 2). The specific effect was also detected at the family, Poaceae and species levels, *Hordeum marinum* (HOMA). The specific effects of the Grass/Poaceae/HOMA groups on LEMA consistently reinforced competition (Table S7). Similarly, cross-trophic interactions were well described by the guild-level effect, with a taxonomic-specific positive effect appearing only from the 'beetle' group/Nitidulidae family for the focal species LEMA in 2020 (Figure S15). Taxonomic-specific HOI was only detected for LEMA's intraspecific interaction, which was negatively impacted by the presence of the 'Bee' group in 2020. This effect was only detected when the neighborhood was grouped at the functional group level.

3.2 | Negative and Positive Interactions Are Equally Prevalent

The likelihood that a guild-level interaction was positive or negative varied based on the interaction types (Figure 3 and Table S7). Interspecific plant interactions were dominantly negative except for HOMA. Pollinators had mainly positive impacts on plant performance (minimum of 24.38% ± 0.19% of positive effect for *Centaurium tenuiflorum* (CETE) in 2021, where the values denote the mean ± standard deviation across groupings) and up to 96.48% ± 6.11% for LEMA in 2021 (Table S7). Intraspecific plant–plant and herbivore impacts were a mix of positive and negative effects, where intraspecific effects varied substantially by focal plant species and year (Figure 3), from 79.94% ± 0.51% of positive effects for HOMA in 2019 to 1.76% ± 0.18% in 2020. Similarly, we found that herbivores had negative and positive effects depending on the environmental context, with the smallest percentage of positive effect across any focal species and year of 8.7% ± 0.9% for LEMA in 2019 (Figure S16).

3.3 | Interaction Strength has Relatively Weak Effects on Performance

The effect of each trophic guild on plant performance was relatively weak and depended on the interaction type (Figure 4 for functional grouping, or Figure S17 for all grouping factors). Interspecific plant individuals had the most variable effects, with guild-level effects negatively impacting performance up to 33.9% ± 16.7% (LEMA in 2019) and taxonomic-specific effects up to 44.8% (Poaceae for LEMA in 2019; Table S8). While most of the estimated effect strengths of pollinators and herbivores were weak (4), and thus centred around 0, they commonly impact 10%

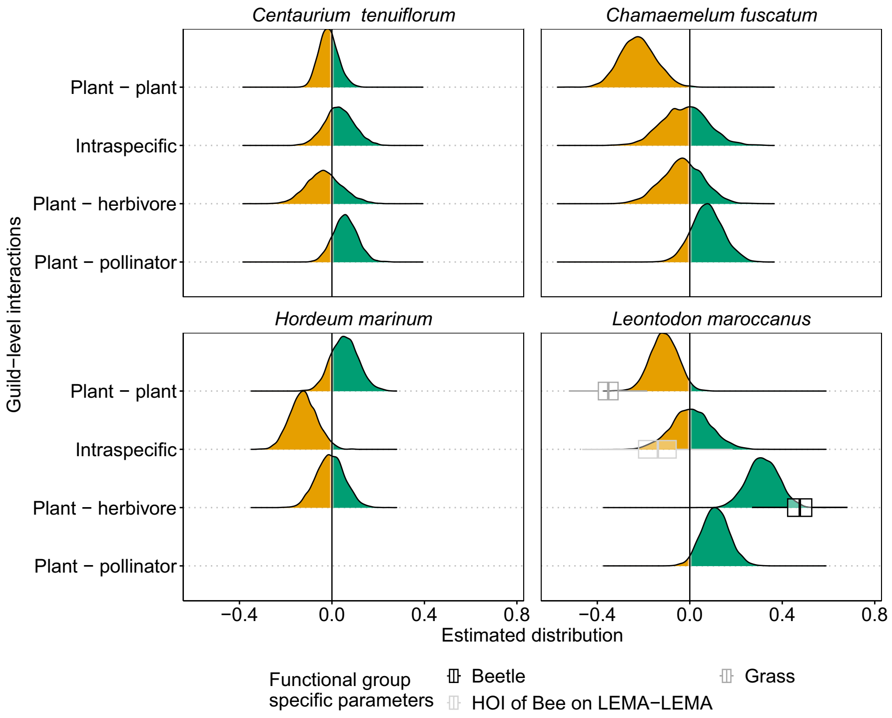

FIGURE 2 | Distribution of guild-level species interactions and their functional group-specific interactions, if relevant, for the year 2020. Orange represents negative interactions, and green represents positive interactions. All years and grouping levels are shown in Figure S13.

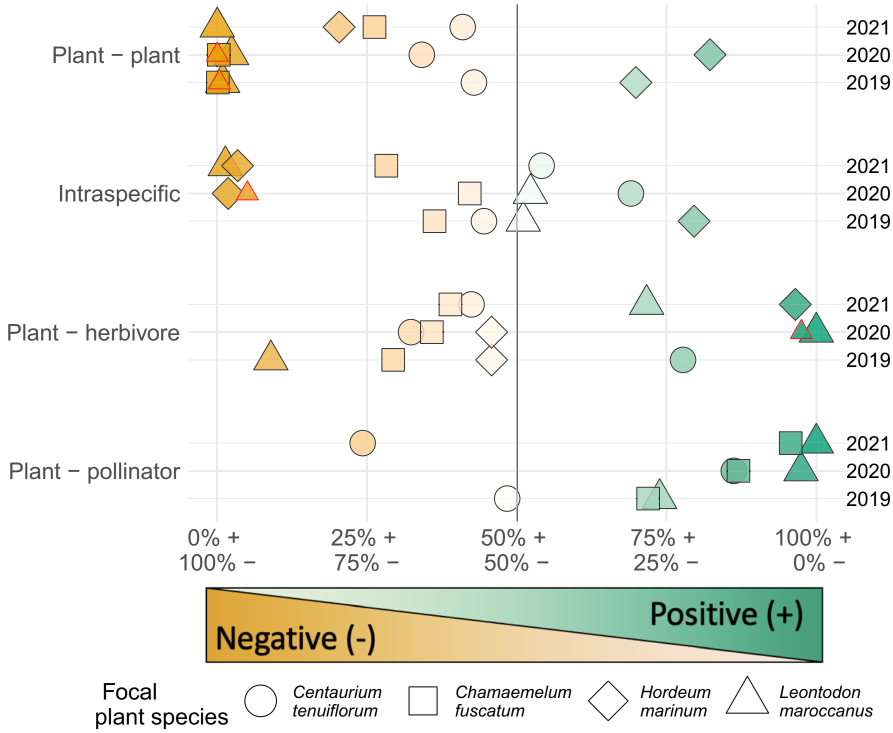

FIGURE 3 | Percentage of positive versus negative effects depends on the focal species and interaction type. Each interaction is situated on the spectrum, from mainly positive (CHFU, plant–pollinator, 2021) to mainly negative (LEMA, plant–plant, 2021) or neutral (CETE, plant-pollinator, 2019). Plant function groups with specific interactions (circled in red) are always strongly competitive when present (e.g., Grass on LEMA). The points encircled in red are functional group-specific interactions acting on the focal designated by their shape. Results depict species grouped by functional group. All grouping levels are shown in Figure S16.

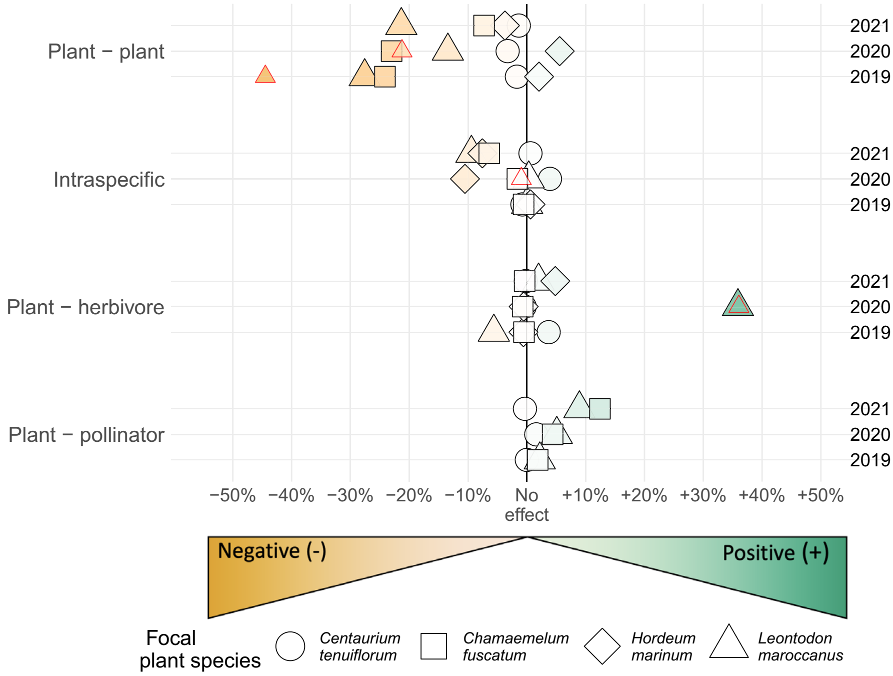

FIGURE 4 | Realised averaged effect of species interaction on individual performance in percentages (%), weighted by the mean number of individuals observed in each trophic level. The strength and direction of species interaction depend on the focal species and trophic level. The points encircled in red are functional group-specific interactions acting on the focal designated by their shape. More specifically, we see 'grass' specific competitive effect on LEMA, 'bee' specific-HOI effect on LEMA's intraspecific interaction and finally, 'beetle' specific positive effect on LEMA. Results depict species grouped by functional group. All grouping levels are shown in Figure S17.

of a focal's performance (realized alpha of 0.1), with one particular year, where herbivore increases LEMA's performance by 34.9 ± 2.8. The taxonomic-specific effects, 'beetle' group/Nitidulidae family, further reinforced the positive effect of herbivores on LEMA in 2020 (Figure 4). Relatively, the observed HOI effect of 'bees' on LEMA's intraspecific interaction in 2020 was small, with only an average of 0.9% decrease in performance. Despite the low strength of most positive effects on performance, they collectively yielded substantial overall impacts. Interestingly, positive interactions are not the by-product of a single highly abundant species (Figure S11).

4 | Discussion

By combining multiple years of extensive field data collection in a Mediterranean grassland with a new method for estimating the nature and strength of species interactions (Weiss-Lehman et al. 2022), our study quantifies the importance of four common types of ecological interaction while allowing for higher-order interactions on plant performance. Our results are based on an adaptive and computational robust modeling approach, which can be applied in highly diverse systems without over-fitting the model. They show, at least for our system, that cross-trophic interaction types, while overall weak, vary from positive to negative signs. Only a few taxonomic-specific direct interactions and cross-trophic HOIs were needed to characterize plant reproductive success within our study system. These patterns were robust to the different groups we examined, regardless of grouping at the species, family, or functional group. Our result provides a welcome starting point for other researchers when deciding how to simplify potential interactions to include in diverse, multitrophic models—especially if applying non-sparse statistical frameworks, where models would fail to converge if including all potential species interactions.

Detailed exploration of guild-level direct terms points to a more nuanced story. Our findings suggest that though most species within trophic guilds have redundant effects, one individual term at the species, family or functional group level often emerged as diverging from the relevant guild-level term. Such taxonomic-specific terms often coincided with dominant species. Further, while there was strong evidence that the nature of guild-level direct interactions varied extensively between positive and negative (Figure 3), most net, abundance-weighted effects were very weak (Figure 4), except for interspecific plant–plant interactions, which tended to be strongly negative (i.e., competitive). Our study clearly shows that most single species within a trophic level do not have distinct effects on plant performance, but some species do, and these distinct effects are strong and important.

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

Identifying the key taxonomic groups that exhibit a divergent interaction effect from their trophic guild has important ramifications for ecological theory and conservation strategy (Walker 1992). For instance, the "beetle" group and the Nitidulidae family in particular, were found to have a specific positive effect on *Leontodon maroccanus* (LEMA) in 2020. Within the Nitidulidae family, the genus *Brassicogethes*, also known as pollen beetle, is the most abundant in our system (Figure S9). These beetles are generalist pollen and nectar feeders (Seimandi Corda et al. 2018), with adults and juveniles moving around flower heads (Wäckers, Romeis, and van Rijn 2006). Yet, they are specialized on the Brassicaceae plant family for oviposition (Seimandi Corda et al. 2018). The negative impact of flower beetles may be mainly restricted to their host plant, as suggested by Seimandi Corda et al. (2018), and act as pollinators in other instances, especially facilitating pollen transport within a single flower in self-compatible plants such as LEMA (Hurtado, Godoy, and Bartomeus 2023). Additionally, we found that grasses, when grouped at the functional level ('Grass'), family level (Poaceae) or species level (*Hordeum marinum*, HOMA), had an effect that diverged from other heterospecific plants on LEMA. While plant interactions are dominantly negative, the specific effect of grass individuals reinforced such competition. LEMA and HOMA are the most abundant in this system, which could explain their strong competitive effect; we speculate this could occur in other grassland ecosystems as the Poaceae and Asteraceae families have distinct ecological strategies leading them to be efficient invaders in many systems around the world (Huang et al. 2024). Understanding if these families can coexist with the rest of the plant community despite their strong competitive abilities or are slowly excluding others from the system is critical to predicting the accurate state of the community and potentially managing it (Aoyama et al. 2022).

Similarly, understanding the importance of higher-order interactions in the speciose multitrophic systems needs further attention. We found little evidence of the importance of HOIs despite the one occurrence in 2020, for LEMA. The effect of the 'bee' grouping on LEMA reinforced intraspecific competition yet had a marginal realized effect on its performance (< 1%). Negative effects of pollinators on intraspecific interaction can occur through dilution effect (Benadi and Pauw 2018) and/or stronger competition for the attention of potentially scarce pollinators (Lázaro, Lundgren, and Totland 2009). Despite the high sensitivity of detecting HOIs with our approach, based on simulated data (95.6%, Appendix S4.12), few HOIs were detected in our system. The lack of detectable HOIs is perhaps surprising as there is evidence of their importance in other systems (e.g., Mayfield and Stouffer 2017; Bimler and Mayfield 2023). A notable difference between our studies and others is the use of aggregate groups of species and the inclusion of multiple trophic levels. HOIS may be more detectable with only species-level groupings. Given the different approach we used to other studies, it is important to note that our study does not conflict with other empirical studies that have found significant HOIs (Buche, Bartomeus, and Godoy 2024), or theoretical within-guild models (Mayfield and Stouffer 2017; Barbosa, Fernandes, and Morris 2023; Lai et al. 2024). Certainly, our results suggest the need for further investigations of the importance of HOIs in complex natural communities.

Previous studies investigating species interactions have restrained them to a priori directions in their effects (Gómez, Iriondo, and Torres 2023; Bimler et al. 2023). Allowing for interactions to vary along a continuum of positive-to-negative effects revealed that the effect of pollinators on plants was primarily positive while heterospecific plant-on-plant interactions were mainly competitive, as expected (Ollerton et al. 2011; Rodger, Bennett, and Razanajatovo 2021; Adler et al. 2018; Yang et al. 2022); yet, surprisingly, intraspecific plants and herbivore interactions with plants were highly variable, including some strong positive effects. Given that we used seed set as our proxy for performance, a positive effect from herbivory may have resulted from the allocation of more energy to seed production due to the stress induced by leaf damage (Bartomeus, Gagic, and Bommarco 2015), or increased growth in compensation for the removal of aging (or young) tissues. Similarly, the positive effects of some intraspecific plants counter most theoretical expectations. Still, such positive effects are commonly observed in nature, especially in populations persisting at low densities (aka Allee effect) (Heyes et al. 2020; Bowler et al. 2022) or in the presence of favorable micro-environments (Bimler et al. 2018). While positive interactions among individuals of the same species can lead to uncontrolled population growth (Hart 2023), this positive-feedback loop may be limited by negative effects from individuals of different species (Sheley and James 2014), the presence of higher trophic levels (Cervantes-Loreto et al. 2021), or temporal variations in the direction of interactions within the same species (Zou, Yan, and Rudolf 2024), as evidenced in this study.

Except for heterospecific plants, the overall net strength of species interactions across trophic levels was weak, suggesting an emerging neutrality in our system. This finding is aligned with classic ecological theory, which posits that the feasibility and stability of ecological systems are promoted by weak species interactions (May 1972; Yang et al. 2023). The effect of the heterospecific plants was, however, strong in some instances—showing a potentially strong competition for resources in a system with strong annual climatic variation. While the 3 years considered have relatively similar precipitation regimes (Figure S3), explicitly accounting for interannual precipitation variation might elucidate additional mechanisms of such competition (Bimler et al. 2018; Hallett et al. 2019). Indeed, the tendency of our system towards neutrality might indicate that fluctuation-dependent mechanisms, such as the spatial and temporal storage effect (Tan et al. 2017) or relative non-linearity (Hallett et al. 2019), could play an important role in driving coexistence in our system. Without further study, however, our results cannot be used to determine which, if either, of these mechanisms is involved in maintaining the diversity of this system, but targeted experiments to test for these mechanisms are a high priority for future studies.

Overall, our findings provide critical empirical evidence on the nature and strength of species interactions in a highly-speciose ecosystem. Our system presents, on average, guild-level weak effects rather than being involved in complex sets of pairwise and higher-order interactions. As these effects range from positive to negative interactions, they should not be predefined with one specific direction but allowed to vary along a continuum. This does not mean we should study complex systems by assuming a random structure of biotic interactions. Instead, we should identify the redundant effects within trophic guilds and the specific interactions that deviate from this redundancy. This can be particularly important for future theoretical work on diversity and conservation strategies for managing strong competitors. Lessons from this study advance our understanding of the structure of biotic interactions under high-dimensional natural systems.

Author Contributions

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 analyzed 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.

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Data Availability Statement

Data and Code have been deposited on Zenodo, linked to the following Github: https://github.com/Buchel9844/Complexity_Caracoles (V.1). Zenodo. DOI: https://doi.org/10.5281/zenodo.14504277

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.