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RESEARCH ARTICLE

Functional Distance Mediates Plant Interactions

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ABSTRACT

Question: The outcome of plant interactions depends on the physiological, morphological, and reproductive traits harbored by the interacting species. The outcomes of plant interactions depend on: (a) trait dissimilarity mechanisms, whereby species with similar traits compete more intensely due to niche overlap, and (b) trait hierarchy mechanisms, whereby species with higher relative fitness outcompete species with less efficient traits under specific environmental conditions. We hypothesized that the functional distance between interacting species affects the outcome of plant interactions simultaneously through both mechanisms.

Location: We collected 10 Mediterranean herb and shrub species in two locations in central Spain.

Methods: We established a manipulative experiment including 10 species growing in pairs. We estimated neighbor effects by measuring the relative change in values of 13 above- and belowground traits of a focal species caused by the presence of a heterospecific (compared to a conspecific) neighbor. We explored (i) which traits were more affected by neighbors, (ii) which species were more affected by an interacting species, either as focal or neighbor and (iii) how the neighbor effect varied with the functional distance between pairs.

Results: Ten out of thirteen traits varied in the presence of a heterospecific (compared to a conspecific) neighbor, six of them increasing (e.g., total photosynthetic area, number of root nodules, root weight) and four decreasing their values (e.g., leaf and root C content). The relative change of trait values in heterospecific pairs significantly increased as functional distance decreased for most plant-performance traits. Only root biomass showed the opposite trend.

Conclusion: Trait hierarchy mechanisms prevailed but trait dissimilarity mechanisms operated on specific root traits, indicating that both simultaneously determine the outcome of interactions. The heterogeneity of neighbor effects responded mainly to differences between above- and belowground traits, reinforcing the need to consider them both for a mechanistic comprehension of community dynamics.

1 | Introduction

Understanding how traits mediate the outcome of plant interactions is crucial for comprehending the mechanisms involved in community assembly (McGill et al. 2006; Wright et al. 2004; Adler et al. 2013). Plant traits encapsulate the evolutionary, ecological, physiological, and morphological information that characterizes plant species identity (Cadotte et al. 2011). The link between plant functional traits and the fitness of each plant is established through its different components, including growth, reproduction, and survival. In this sense, mechanisms of trait dissimilarity and trait hierarchy may arise when certain traits react to changes induced by neighbor plants (response traits *sensu* Violle et al. 2007).

The reciprocal effects of neighbor plants will largely depend on their trait differences (Grime 2006; Mayfield and Levine 2010). Trait dissimilarity mechanisms occur when species with similar traits compete more intensely than species with different traits (Macarthur and Levins 1967; Mason et al. 2007; Wilson and Stubbs 2012). Alternatively, trait hierarchy mechanisms act when species harboring particular traits have a functional advantage over species with different traits conferring lower relative fitness under specific environmental conditions (Fort et al. 2014; Kraft et al. 2015; Carmona et al. 2019). Trait dissimilarity and hierarchy mechanisms mediate the outcome of species interactions through niche differences and relative fitness differences, respectively (Mayfield and Levine 2010).

Mechanisms of trait dissimilarity have been traditionally proposed as the main factor explaining the outcome of plant interactions in ecological communities. However, according to population growth rate models, stabilization forces also induce the prevalence of trait hierarchy mechanisms (Adler et al. 2007). For instance, coexisting plant species in a Neotropical dry forest were similar in four leaf and wood traits (leaf area, specific leaf area, leaf succulence, and wood specific gravity), but dissimilar in traits related to adult morphology and regeneration niches (maximum height and seed mass) (Swenson and Enquist 2009). Trait dissimilarity and hierarchy mechanisms have been reported to act together affecting plant interactions, with hierarchies prevailing during early stages of plant development and shifting into trait complementary patterns as the community undergoes a re-assembly process over time (Wagg et al. 2014). A recent meta-analysis on experiments involving paired plant species growing together revealed that trait dissimilarity mechanisms prevailed over trait hierarchy mechanisms except for pairs of species that usually do not co-occur in nature (Buche et al. 2022). In other studies, trait hierarchy rather than trait dissimilarity mechanisms were reported as the main determinants of plant interactions (Kraft et al. 2015; Carmona et al. 2019). In summary, the evidence on the relative importance of the mechanisms driving the outcome of plant interactions (trait dissimilarity, trait hierarchy, or both mechanisms) is still to be determined.

Based on the observations above, we hypothesize that the functional distance between species might affect the outcome of plant interactions simultaneously through trait dissimilarity and trait hierarchy mechanisms. We aimed to understand how morphological, physiological, and reproductive plant traits are affected by heterospecific interactions. For that purpose, we compared trait values of focal plants growing with a heterospecific neighbor versus a conspecific neighbor. Utilizing conspecific pairs as controls for heterospecific interactions, as opposed to using plants alone, enables the isolation of species-specific effects from those associated with plant density. We selected several traits that cover above- and belowground morphological and physiological characteristics to test whether trait dissimilarity and trait hierarchy mechanisms act differentially across distinct traits (Carmona et al. 2019). We specifically analyzed the neighbor effect on 10 focal species for 13 seedling and adult traits to assess: (i) which traits are more affected by neighbors–i.e., overall neighbor effect-, (ii) which focal species are more affected by neighbors (Figure 1a, left), and conversely, which neighbor species cause more effects on focal plants (Figure 1a, right)–i.e., species-specific neighbor effect- and (iii) whether the neighbor effect varies with the functional distance between the pair of species–i.e, functional distance-mediated neighbor effect (Figure 1b).

2 | Material and Methods

We followed the procedure depicted in Appendix S1 and explained in depth below.

2.1 | Selecting and Phenotyping Plant Species

To select the species for the pairwise plant interaction experiment (Section 2.2), we initially collected 42 Mediterranean herbs and shrubs from May to September 2020 in two natural locations: Torrelodones, Madrid, Spain (decimal geographic coordinates: 40.59, −3.93), and Sierra Ministra, Castilla la Mancha, Spain (41.02, −2.37). These areas are characterized by granite lithologies and limestones of cold semi-arid steppes (Bsk, Köppen climate classification). We carried out germination assays for the initial set of 42 species, and selected 10 short-lived species with high germination rates. These species belonged to distinct evolutionary clades trying to capture a wide range of functional dissimilarities: *Trifolium angustifolium* (Fabaceae), *Vicia villosa* (Fabaceae), *Bromus tectorum* (Poaceae), *Hordeum murinum* (Poaceae), *Andryala integrifolia* (Asteraceae), *Helichrysum stoechas* (Asteraceae), *Thymus mastichina* (Lamiaceae), *Micropus erectus* (Asteraceae), *Hirschfeldia incana* (Brassicaceae) and *Plantago coronopus* (Plantaginaceae).

In order to phenotype these 10 species, we measured seed, seedling, and adult functional traits (Appendices S2 and S3). Seed size and weight were measured with the help of a binocular stereoscope (Leica Microsystems M80, Germany) and an analytical balance (Denver Instrument S-234, Germany). Seed size measurements were performed on 10 seeds of each species. Small seeds were weighed in groups of 50. To measure seedling and adult traits, we carried out a greenhouse assay in pots, from February until August 2021. Seeds from all species were sown in alveolus trays. We then transplanted 60 seedlings into 30 pots, two individuals per pot and three pots per species. Thus, we measured the traits from six individuals per species. Traits of seedlings (i.e., individuals with cotyledons) were measured the first month following emergence. Adult traits were measured

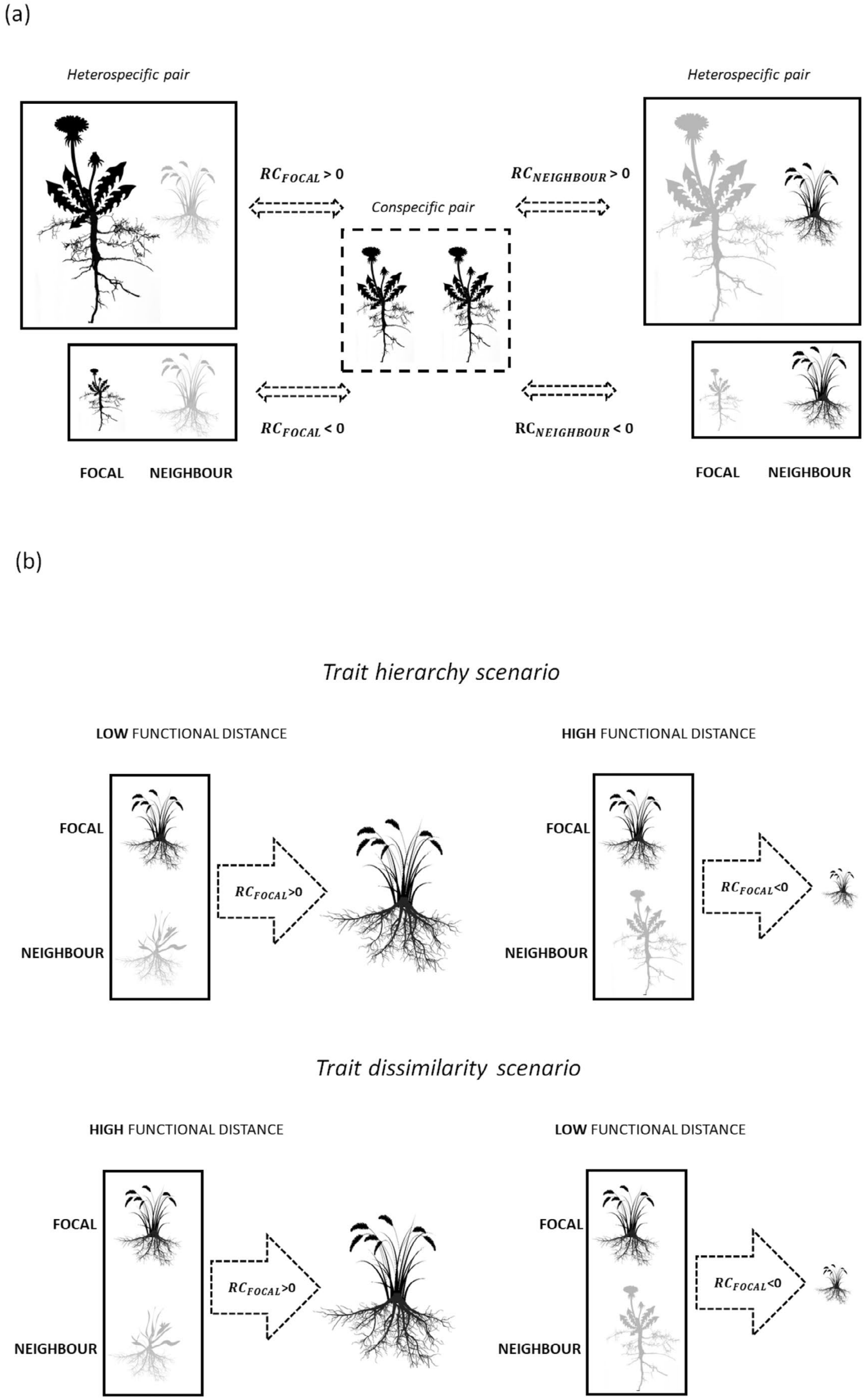

FIGURE 1 | Legend on next page.

FIGURE 1 | Schematic representation of the neighbor effects on plant traits and the relationship with functional distance between focal and neighbor species. The focal plant is the individual whose trait variation is measured because of the presence of a neighbor. Conversely, the neighbor plant is the individual that generates the effect on the focal plant. We quantified the neighbor effect as the relative change (RC) of a trait when the individual grows with a heterospecific compared to when it grows with a conspecific. Therefore, RC_{focal} is the relative change that the focal plant undergoes because of growing with a heterospecific, whereas $RC_{neighbour}$ is the relative change that a plant produces on the focal plant. Positive (negative) RC_{focal} values indicate that plants growing with heterospecifics have higher (lower) trait values than those growing with conspecifics (Panel a, left). Similarly, neighbor plants producing higher (lower) trait values in focal plants have positive (negative) $RC_{neighbour}$ values (Panel a, right). Furthermore, the functional distance between the paired individuals can mediate the outcome of the interaction following two possible mechanisms: Panel b, top) Trait hierarchy mechanisms arise when neighbor effects become more negative with the functional distance between the individuals (e.g., tall plants have a negative effect on short plants). Panel b, bottom) Trait dissimilarity mechanisms arise when the neighbor effect is more negative in functionally similar species (e.g., a plant with shallow roots will have more negative effects on a plant with shallow roots than on a plant with deep roots).

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before harvesting at the end of the assay when individuals reached mature stages.

Soil used as substrate for this assay was collected in La Canaleja Agricultural Research Field Station, located in Alcalá de Henares, central Spain (geographic coordinates: 40.51, −3.31). The area is semi-arid, with low and irregularly distributed rainfall (annual average of 353 mm). Soils are Calcic Haploxeralfs, with a sandy-loam texture, neutral (pH of 7.9), non-saline (0.123 dS m^{-1}) and with low contents of total organic carbon (7.5 g kg^{-1}) in the topsoil layer (Martín-Lammerding et al. 2015). Soils were collected in February 2021 at depth of 5–20 cm (to avoid seed bank in the topsoil centimeters) and sieved through a 5 mm mesh. Soil was heated at 120°C for 1 h to reduce the microbial load and mixed with silica sand at 9:1 vol/vol.

We used this trait information to calculate the functional distance between the neighbor and the focal species of each pair in the experiment described in Section 2.2. This was performed in order to avoid circularity in the statistical analyses (i.e., employing the same trait values both as responses and as effects in the statistical models).

2.2 | Pairwise Plant Interaction Experiment

A greenhouse experiment was established to measure neighbor effects in the 10 short life- span species selected in Section 2.1. With 10 different focal species, we obtained 45 heterospecific pairs and 10 conspecific pairs that were replicated 6 and 3 times, respectively. This gave 300 pots in total (270 heterospecific and 30 conspecific), with two individuals per pot. Fifty pots (100 individuals) were not measured due to death of the individuals (Appendices S4–S6).

Soil used as substrate for the experiment was collected and processed as described above. Pots (12 × 25 × 18 cm) were filled with this mix (5.7 L) and left to stabilize for 30 days until seeding on 10th February 2021. We selected 2–5 seeds per species sown at 1 cm depth to ensure the germination of at least one individual per species and pot. When more than one individual per species emerged, the surplus seedlings were removed, retaining only one individual. Watering lasted from March 2021 to July 2021 and added at a rate of 1.8 ± 0.2 L/m^2 per day distributed in 3 pulses of 5 min, 5 days a week. Radiation was homogenous due to shade cloths placed on top of the greenhouse. The temperature of the greenhouse was set to 22°C degrees using a heating/cooling system.

2.2.1 | Trait Measurement

The plant interaction experiment lasted 4 months, and all plant individuals were harvested and processed from 22th June to 30th July 2021. For all individuals, which were grown until the reproductive stage, we measured 13 above- and belowground morphological, physiological and reproductive traits (Table 1). The number of traits was smaller than that used to phenotype the species (Section 2.1) since in this case we could only consider adult traits.

A total of 244 leaf and root samples (for which we had enough material) were dried at 60°C and ground. C and N contents were measured with an ELEMENTAL LECO TruSpec CN elemental analyzer (LECO, Michigan). All these traits are ecologically relevant as they are related to plant fitness (growth, survival, and reproduction) as well as to different ecosystem functions (Table 1).

2.2.2 | Neighbor Effects

In each pot, the individual whose traits were affected the most by the other individual was identified as the focal plant, whereas the individual that caused the influence was referred to as the neighbor plant. Both individuals of each pair were measured because they were both simultaneously producing and receiving neighbor effects due to the mutual interaction.

To quantify the neighbor effect, we compared the relative change (RC) in the trait value of a focal individual caused by a heterospecific neighbor contrasted with the changes induced by a conspecific neighbor (Equation 1).

$$RC_{i,j,t} = \frac{t_{ij} - \overline{t_{ii}}}{\overline{t_{ii}}} \tag{1}$$

where $RC_{i,j,t}$ refers to the relative change in the trait t caused in the focal individual of the species i by the individual of the neighbor species j; tij is the trait value of the focal individual of the species i growing with the neighbor individual of the species j; and $\overline{t_{ii}}$ is the average of the trait values of the six individuals

TABLE 1 | Ecological relevance of the 13 plant traits measured in the greenhouse experiment. Class 1 characterizes each trait according to the plant part where it is located whereas class 2 classifies each trait as morphological if it corresponds to a structure or physiological if it is directly associated with a function. Bibliography consulted: (1) Bjorkman et al. 2018; (2) Hanisch et al. 2020; (3) Cornelissen et al. 2003; (4) Falster et al. 2011; (5) Foyer 2003; (6) Bardgett et al. 2008; (7) De Long et al. 2019; (8) De Deyn et al. 2008; (9) Chen et al. 2019; (10) Lavorel et al. 2007; (11) Averill et al. 2014; (12) Legay et al. 2014; (13) Nunes-Nesi et al. 2010; (14) Carrillo et al. 2017; (15) Grigulis et al. 2013; (16) Garnier and Navas 2012; (17) Reich 2014; (18) Wright et al. 2004; (19) Tang et al. 2019; (20) Burton et al. 2002; (21) Reich et al. 2008; (22) Sun et al. 2020; (23) Faucon et al. 2017; (24) Fry et al. 2019; (25) Roumet et al. 2016; (26) Pei et al. 2016; (27) Barel et al. 2019; (28) Oreja et al. 2020; (29) Aerts and de Caluwe 1997; (30) Liu et al. 2016; (31) Ferlian et al. 2017.

Plant trait	Units	Class 1	Class 2	Ecological relevance	References
Plant height	mm	Aboveground	Morphological	Proxy of aboveground and biomass production. Influence in nutrient acquisition and fertility. Proxy of light interception and competitive ability and fecundity	1, 2, 4,10, 16
Plant weight (fresh)	g	Whole plant	Morphological	Related to plant productivity	4
Aboveground weight (fresh)	g	Aboveground	Morphological	Proxy of aboveground biomass and nutrient metabolism	7, 15, 17, 18
Specific leaf area (SLA)	cm^2/g	Aboveground	Morphological	Proxy of nutrient acquisition, plant biomass, and fertility. Influence in canopy structure	1, 2, 4, 6, 7, 8, 9, 10, 23, 30
Total photosynthetic area	cm^2	Aboveground	Physiological	Proxy of photosynthetic metabolism, influence in aboveground nutrient storage, biomass production, and leaf energy. Related with canopy structure	1, 2, 3, 4
Number of flowers	n	Aboveground	Morphological	Proxy of fertility	10
Root length	mm	Belowground	Morphological	Proxy of belowground biomass. Influence in soil exploration and erosion resistance	2, 4, 6, 7, 8, 9, 10, 12, 13, 14, 16
Root weight (fresh)	g	Belowground	Morphological	Proxy of belowground biomass and nutrient metabolism	7, 15, 25
Number of root nodules	n	Belowground	Morphological	Related to symbiosis with nitrogen fixers and nutrient acquisition	6, 7, 8, 9, 11
Leaf carbon (C) content	g/100 g	Aboveground	Physiological	Proxy of plant biomass, fertility, and nitrogen metabolism. Influence in competitive strength	2, 3, 9, 13, 27
Leaf nitrogen (N) content	g/100 g	Aboveground	Physiological	Proxy of plant biomass, fertility. Influence on carbon metabolism and competitive strength of the plant	1, 2, 3, 6, 7, 9, 13,17, 24, 26, 27, 28
Root carbon (C) content	g/100 g	Belowground	Physiological	Proxy of nitrogen metabolism and influence in plant growth and development and shoot dry weight	3, 5, 6, 7, 12, 13, 21, 23, 29, 31
Root nitrogen (N) content	g/100 g	Belowground	Physiological	Influence in carbon metabolism plant growth and development. Affects root biomass allocation	2, 6, 7, 8, 9, 13, 19, 20, 21, 22, 23, 24

growing in conspecific pairs. The use of $\overline{t_{ii}}$ as a baseline to compare interspecific interactions, instead of focusing on a single individual, allows incorporation of intraspecific competition at the same density as interspecific competition.

Positive (negative) RC values are indicative of heterospecific neighbors increasing (reducing) trait values of the focal species more than conspecific neighbors (Figure 1a). RC values equalling zero indicate no effect of the neighbor over the focal species trait. Since the RC involves two individuals (focal and neighbor), the identical value can be interpreted both as the RC experienced by the focal individual (RC_{focal}) and as the RC caused by the neighbor individual ($RC_{neighbour}$). As the interaction is paired, we measured both individuals acting as focal and as neighbor.

The ecological interpretation of the increase (or decrease) in RC varies depending on the trait considered. For most traits (e.g., aboveground biomass, total photosynthetic area, and root biomass), if the presence of a heterospecific neighbor increases the trait values of the focal plant species compared to the presence of a conspecific neighbor, this can be interpreted as intraspecific competition being more intense than interspecific competition. However, for other traits, the opposite statement may apply. For instance, leaf carbon contents increase under nutritional (N and P) stress (Radin and Eidenbock 1986). Thus, an increase in the RC values of leaf C might indicate higher nutritional stress when coexisting with a heterospecific compared to a conspecific neighbor, suggesting increased interspecific competition. Similarly, the number of root nodules in legumes increases as the contents of soil mineral N decrease (Goh et al. 2016; Zhao et al. 2020). Legumes increase the number of nodules in the presence of non-legume species compared to conspecifics (Zhao et al. 2020) as a way to avoid competition (i.e., obtaining N from other sources), thus an increase in RC values in the number of nodules can be interpreted as a signal of interspecific competition. In addition, some traits might show opposing patterns depending on the environmental conditions. As an example, competition in shaded environments can increase the specific leaf area while decreasing plant biomass (Liu et al. 2016).

To analyze neighbor effects, we first tested whether the mean neighbor effect on each plant trait (i) was significantly different from zero, and (ii) differed between groups of traits (i.e., above- vs. belowground traits; morphological vs. physiological traits) through *t*-test analyses with the *t.test* function in R v 4.1.2. Then, we searched for species-specific neighbor effects by averaging the RC values of each trait within each species. We obtained the mean RC of each trait per focal species (i.e., the changes experienced by focal plants) and for each neighbor species (i.e., the changes induced by neighbors). We finally checked whether the RC experienced by focal plants, or the RC induced by neighbors, were consistent across traits through a repeatability test performed with the *rpt* function of the rptR package for R (Nakagawa and Schielzeth 2013).

2.2.3 | Functional Distance Mediates Plant Interaction

We calculated the functional distance between each pair of interacting species using the trait data produced at the species level (Section 2.1). The functional distance between two species was calculated with the *gowdis* function in the FD package for R (Laliberté et al. 2014), which allows measurement of the functional distance considering both quantitative and categorical traits from a trait value matrix. *gowdis* calculates the Gower similarity coefficient described by Podani (1999) and afterward transforms it into a dissimilarity coefficient.

Generalized Linear Mixed Models using Template Model Builder (glmmTMB) were used to evaluate whether neighbor effects were dependent on the functional distance between the focal and its neighbor plant. We applied a two-sided formula for model calculation (Equation 2).

$$RC_{focal,\,t} \sim FD_{focal-neighbour} + (1 \mid focal) + (1 \mid neighbour) \qquad (2)$$

where $RC_{focal,t}$ is the RC value of the trait *t* measured in the focal individual, FD is the functional (Gower) distance between focal and neighbor individuals. The final two terms in brackets represent the random effects of the model, defined as the identity of the focal and neighbor individuals respectively.

The dependent variable RC_{focal} was transformed to achieve a normal distribution of residuals. Analyses were run with the function glmmTMB from glmmTMB package for R (Brooks et al. 2017).

3 | Results

3.1 | Overall Neighbor Effects

According to RC values, 10 out of the 13 traits analyzed were significantly affected by heterospecific neighbors, either positively ($RC_{focal} > 0$) or negatively ($RC_{focal} < 0$) (Figure 2). Traits whose values increased in the presence of a heterospecific neighbor were the total photosynthetic area, number of root nodules, root weight, plant weight, aboveground weight and root N content (Figure 2). In contrast, traits whose values decreased in heterospecific combinations were the leaf and root C content, plant height and root length (Figure 2). Only three traits (number of flowers, leaf N content and SLA) were unaffected by heterospecific neighbors, according to their RC values not departing significantly from zero (Figure 2). Taking groups of traits, aboveground traits ($RC_{focal} = 0.27 \pm 0.053$) presented higher values than belowground traits in the presence of a heterospecific neighbor ($RC_{focal} = 0.11 \pm 0.016$; $T = 15.58$ $D.F = 2949$, $p < 0.001$), as did morphological traits ($RC_{focal} = 0.091 \pm 0.015$) compared to physiological traits ($RC_{focal} = 0.027 \pm 0.007$; $T = 8.78$; $D.F = 2460$, $p < 0.01$).

3.2 | Species-Specific Neighbor Effects

Focal species experienced neighbor effects of different sign and magnitude depending on the trait measured (Table 2, top). For example, *H. incana* growing with heterospecific neighbors greatly increased its total photosynthetic area ($RC_{focal} = 7.96$) but decreased its root length ($RC_{focal} = -0.10$). This inconsistency across the RC values for different traits within a species was supported by the non-significant repeatability test ($RC_{focal} = 0 \pm 0.029$, 95% confidence interval = [0, 0.101]).

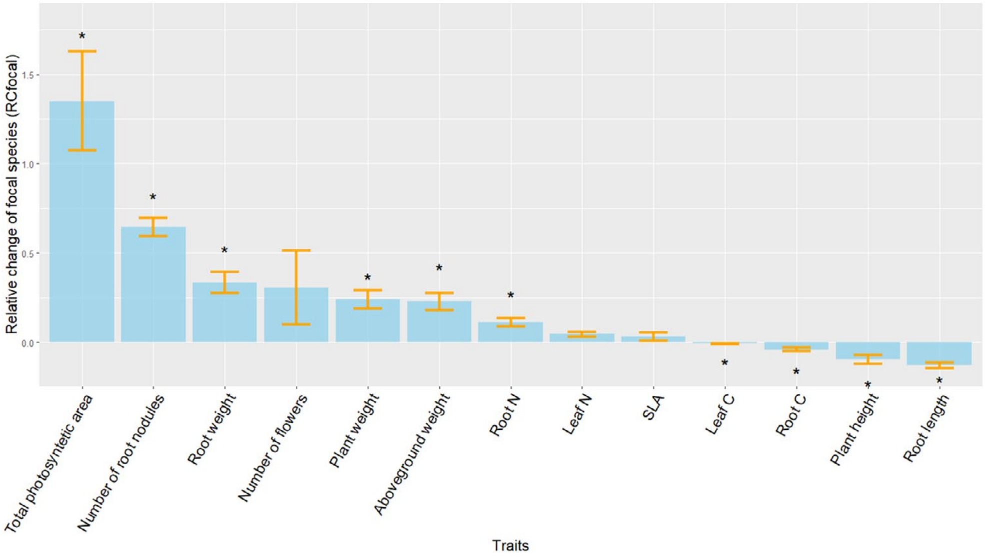


FIGURE 2 | Overall neighbor effects for all focal species on 13 plant traits. Relative change (RC_{focal}) of different focal traits and its significance level (* indicates $p < 0.05$). Negative RC values represent a reduction of the focal trait value and positive RC values an increment of the focal trait value due to the neighbor effect. Brackets represents the sum of mean values plus standard error.

Similarly, a given neighbor species caused effects on focal plants of different sign and magnitude depending on the traits analyzed (Table 2, bottom). For example, *A. integrifolia* caused higher root weights ($RC_{neighbour} = 0.93$) but lower root C contents ($RC_{neighbour} = -0.12$) on its focal plants. Again, the inconsistency of these effects across traits within species was supported by a non-significant repeatability test ($RC_{neighbour} = 0.007 \pm 0.029$, 95% CI = [0, 0.102]).

3.3 | Functional Distance-Mediated Neighbor Effects

The effect that focal plants received from neighbors (RC_{focal}) varied with the functional distance between both species. For eight traits (root weight, plant height, aboveground plant weight, plant weight, total photosynthetic area, root length, root C and N contents) this relationship was negative (Table 3). This pattern indicates that the more functionally different the neighboring plant is, the more the focal trait decreases after the interaction. Only for one trait (root weight), we found higher trait values as the functional distant increased, indicating that focal plants tend to be enhanced after the interaction with a functionally different neighbor (Table 3). In most cases, the identity of the focal species was statistically significant, indicating that individuals within the same species tend to have more similar responses than individuals of different species. Similarly, most cases showed that the neighbor identity was significant, indicating that individuals of the same species caused similar effects on their focal species compared to individuals of different species (Table 3).

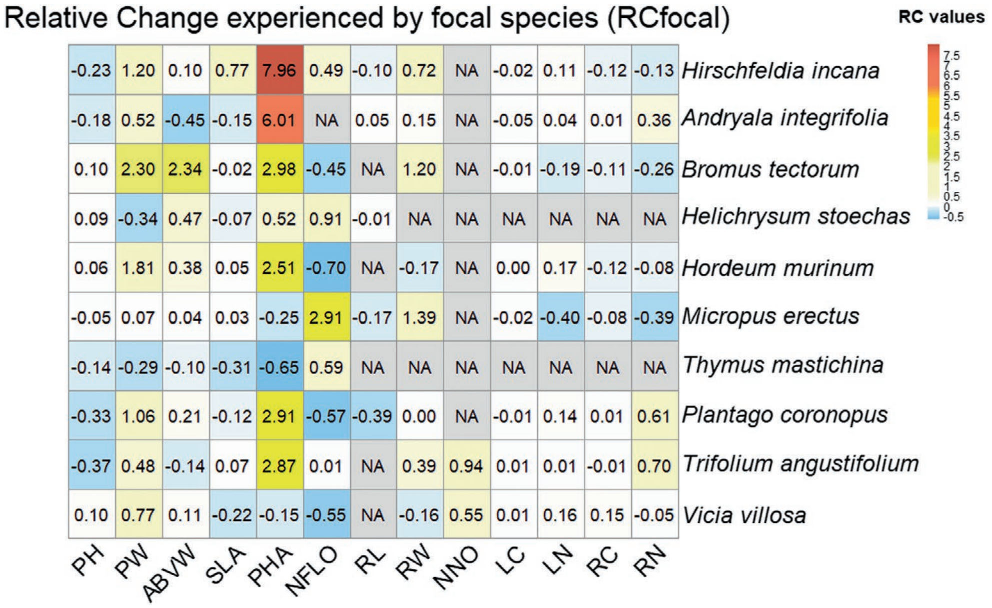
4 | Discussion

Heterospecific interactions were found to impact the trait values of focal plant species, with neighbors exerting significant effects on most traits measured. These neighbor effects either increased or decreased the trait values of focal plants compared to conspecific interactions depending on the trait and the identity of the focal species. In other words, species induced and received inconsistent neighbor effects depending on the species with which they grew. For most of the studied traits (especially biomass-related traits), focal plants growing with a functionally similar neighbor exhibited higher trait values than those growing with a dissimilar one.

In contrast to most experiments studying a limited set of traits (e.g., Bennett et al. 2016; Botta-Dukát 2021), we selected a large number of traits, incorporating a multi-dimensional characterization of plants including aboveground, belowground, morphological, physiological and reproductive measurements. This collection of traits allows a better comprehension of plant performance in pairwise interactions. For example, biomass estimates, apart from reproductive measurements, are a good proxy of plant fitness (Younginger et al. 2017; Carmona et al. 2019). Furthermore, traits related to nutrient content have been shown to inform fundamental trade-offs of ecological processes due to their influence on nutrient acquisition and functional strategies of plants (Swenson and Enquist 2009). We have also considered the importance of the plant ontogenetic stage to correctly characterize functional distances (Cornelissen et al. 2003; Navarro-Cano et al. 2021b) by including seedling and adult traits. But, despite having characterized species with a broad set of traits, our data indicate that accounting for species identity is critical for explaining the outcome of plant interactions. For example, a given focal species might benefit from the interaction with a heterospecific neighbor by growing taller but, at the same time, might be harmed by the limitation of its radical growth. These results indicate that plant identity and trade-offs among traits are determining the outcome of plant–plant interactions. Therefore, a thorough phenotypic characterization of the interacting species is crucial to understand plant interactions (Navarro-Cano et al. 2021a), as we explain below.

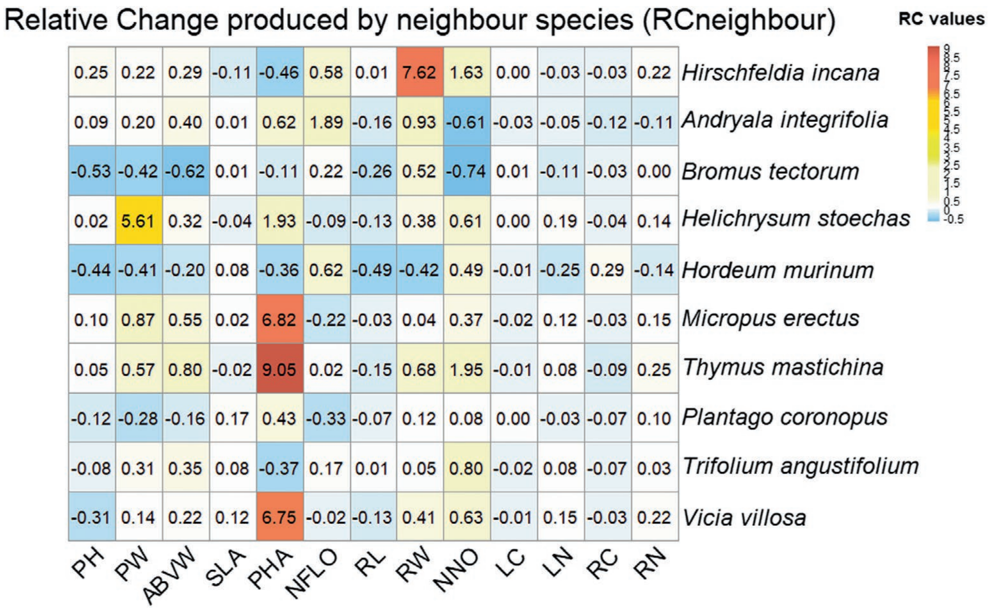
TABLE 2 | Species-specific neighbor effects measured as the relative change experienced by focal species (RC_{focal}) or produced by neighbor species ($RC_{neighbour}$) in 13 traits: plant height (PH), plant weight (PW), aboveground plant weight (ABVW), specific leaf area (SLA), total photosynthetic area (PHA), number of flowers (NFLO), root length (MRL), root weight (RW), number of root nodules (NNO), leaf C content (LC), leaf N content (LN), root C content (RC) and root N content (RN).

Relative Change experienced by focal species (RCfocal)



PH	PW	ABVW	SLA	PHA	NFLO	RL	RW	NNO	LC	LN	RC	RN	
-0.23	1.20	0.10	0.77	7.96	0.49	-0.10	0.72	NA	-0.02	0.11	-0.12	-0.13	*Hirschfeldia incana*
-0.18	0.52	-0.45	-0.15	6.01	NA	0.05	0.15	NA	-0.05	0.04	0.01	0.36	*Andryala integrifolia*
0.10	2.30	2.34	-0.02	2.98	-0.45	NA	1.20	NA	-0.01	-0.19	-0.11	-0.26	*Bromus tectorum*
0.09	-0.34	0.47	-0.07	0.52	0.91	-0.01	NA	NA	NA	NA	NA	NA	*Helichrysum stoechas*
0.06	1.81	0.38	0.05	2.51	-0.70	NA	-0.17	NA	0.00	0.17	-0.12	-0.08	*Hordeum murinum*
-0.05	0.07	0.04	0.03	-0.25	2.91	-0.17	1.39	NA	-0.02	-0.40	-0.08	-0.39	*Micropus erectus*
-0.14	-0.29	-0.10	-0.31	-0.65	0.59	NA	NA	NA	NA	NA	NA	NA	*Thymus mastichina*
-0.33	1.06	0.21	-0.12	2.91	-0.57	-0.39	0.00	NA	-0.01	0.14	0.01	0.61	*Plantago coronopus*
-0.37	0.48	-0.14	0.07	2.87	0.01	NA	0.39	0.94	0.01	0.01	-0.01	0.70	*Trifolium angustifolium*
0.10	0.77	0.11	-0.22	-0.15	-0.55	NA	-0.16	0.55	0.01	0.16	0.15	-0.05	*Vicia villosa*

Relative Change produced by neighbour species (RCneighbour)



PH	PW	ABVW	SLA	PHA	NFLO	RL	RW	NNO	LC	LN	RC	RN	
0.25	0.22	0.29	-0.11	-0.46	0.58	0.01	7.62	1.63	0.00	-0.03	-0.03	0.22	*Hirschfeldia incana*
0.09	0.20	0.40	0.01	0.62	1.89	-0.16	0.93	-0.61	-0.03	-0.05	-0.12	-0.11	*Andryala integrifolia*
-0.53	-0.42	-0.62	0.01	-0.11	0.22	-0.26	0.52	-0.74	0.01	-0.11	-0.03	0.00	*Bromus tectorum*
0.02	5.61	0.32	-0.04	1.93	-0.09	-0.13	0.38	0.61	0.00	0.19	-0.04	0.14	*Helichrysum stoechas*
-0.44	-0.41	-0.20	0.08	-0.36	0.62	-0.49	-0.42	0.49	-0.01	-0.25	0.29	-0.14	*Hordeum murinum*
0.10	0.87	0.55	0.02	6.82	-0.22	-0.03	0.04	0.37	-0.02	0.12	-0.03	0.15	*Micropus erectus*
0.05	0.57	0.80	-0.02	9.05	0.02	-0.15	0.68	1.95	-0.01	0.08	-0.09	0.25	*Thymus mastichina*
-0.12	-0.28	-0.16	0.17	0.43	-0.33	-0.07	0.12	0.08	0.00	-0.03	-0.07	0.10	*Plantago coronopus*
-0.08	0.31	0.35	0.08	-0.37	0.17	0.01	0.05	0.80	-0.02	0.08	-0.07	0.03	*Trifolium angustifolium*
-0.31	0.14	0.22	0.12	6.75	-0.02	-0.13	0.41	0.63	-0.01	0.15	-0.03	0.22	*Vicia villosa*

Note: Negative (positive) RC values indicate a reduction (increase) of the trait value due to the heterospecific neighbor effects. Colors of each cell indicate RC values. NAs indicate RCs that could not be computed due to the mortality of all the individuals or the absence of that trait in its morphology (e.g., root nodules) or phenology (e.g., number of flowers). Mean values and standard error of traits for each species are provided at Appendix S7 Trait correlation matrix is also provided at Appendix S8.

We have shown that the functional distance between species significantly explained the effect of neighbors for most traits (eight out of 13). Except for root weight, the relationship between the neighbor effect and the functional distance between focal and neighbor was negative, suggesting that focal plant trait values were larger when growing with functionally similar species in their vicinity. Similar results have been shown in other studies, suggesting that the outcome of paired interactions is mediated by trait hierarchy rather than trait dissimilarity mechanisms (Adler et al. 2013; Carmona et al. 2019). Swenson and Enquist (2009) showed that functionally similar species could coexist at fine spatial scales when considering leaf area, SLA, leaf succulence and wood specific gravity. Gross et al. (2007) showed that species with similar early germination times and quick growth rates possessed an initial advantage in competitive interactions in comparison with less similar species. Soliveres et al. (2018) showed that species pairs with short functional distances coexisted and grew more than more functionally distant pairs. The rationale of all these results is that functionally close species are likely to be more similar in their functional characteristics than distantly related species and perform similarly under similar environmental conditions (Adler

TABLE 3 | Relationship between effect of the neighbor received by the focal individual (RC_{focal}), and the functional distance (FD) between both species.

Plant trait	Transformation	Family	Estimate ± SD	*z*	*p*
Plant height	sqrt (RC + 1)	Gaussian	−0.89 ± 0.18	−5.04	< 0.001
Aboveground weight	sqrt (RC + 1)	Gaussian	−1.63 ± 0.32	−5.10	< 0.001
Photosynthetic area	log10 (RC + 1.01)	Gaussian	−1.75 ± 0.63	−2.79	0.01
Root N	sqrt (RC + 1)	Gaussian	−0.65 ± 0.25	−2.58	0.01
Root weight	sqrt (RC + 1)	Gaussian	1.09 ± 0.48	2.25	0.02
Plant weight	log10 (RC + 1.01)	Gaussian	−1.94 ± 0.5	−3.92	< 0.001
Root C	RC	Gaussian	−0.67 ± 0.26	−2.58	0.01
Root length	sqrt (RC + 1)	Gaussian	−0.52 ± 0.17	−3.10	< 0.001
Leaf C	RC	Gaussian	0.05 ± 0.05	1.01	0.31
SLA	sqrt (RC + 1)	Gaussian	−0.08 ± 0.12	−0.64	0.52
Flowers	sqrt (RC + 1)	Nbinom1	−0.5 ± 0.75	−0.67	0.50
Nodules	sqrt (RC + 1)	Gaussian	−0.95 ± 1.27	−0.75	0.45
Leaf N	RC	Gaussian	0.15 ± 0.32	0.48	0.63

Note: The estimates of the generalized linear mixed models are shown along their standard error. Traits are ordered from higher to lower values of RC_{focal}-FD model relationship. The identity of both focal and neighbor species was included in the model as random factors. RC were transformed. Residuals from the models are provided at Appendix S9. The code utilized for the analysis described in this study is displayed in Appendix S10.

et al. 2007; Swenson and Enquist 2009). How plants interact and play dominant–subdominant roles according to their trait differences strongly depend on the identity of the interacting species (Soliveres et al. 2018), a pattern our results clearly support. The closer the trait value is to the optimum trait expression under certain conditions, the higher the performance ability and the stronger the negative effect on the functionally distant species would be (Adler et al. 2013). Hence, the negative effects of pairwise interactions can be reduced when the interacting species are functionally similar and exhibit comparable performance advantages (Soliveres et al. 2018).

The only plant trait value that was enhanced by the interaction with functionally distant neighbors was root weight. Differences in root traits are usually related to a reduction of competition, which promotes coexistence (Kraft et al. 2015). In addition, contrasting root phenotypes have been suggested to promote plant facilitation (Navarro-Cano et al. 2021a). As belowground traits are more tightly connected with soil abiotic conditions and nutrients than aboveground traits, they respond faster to changes in the soil environment (Mao et al. 2018). In fact, niche differentiation processes have been argued to be more frequent than expected in the belowground system (Soliveres et al. 2018). Hence, it is not unexpected that trait dissimilarity rather than trait hierarchy mechanisms will be the main mechanism behind plant interaction affecting root weight. Nevertheless, certain belowground traits such as root length followed the opposite trend. Root length is related with fast growth and productivity, characteristics that usually confer a performance advantage per se, favoring trait hierarchy mediated competition (Freckleton and Watkinson 2001).

Although simulation models have addressed this issue (Gallien 2017; Gallien et al. 2017), an experimental approach is still necessary to fully comprehend the outcomes of multispecies interactions influenced by functional distances. Moreover, the conclusions drawn from this experiment are clearly constrained by its pairwise design. Nature, being more complex, often involves interactions within multispecies groups where transitive loops can influence the mechanism of trait hierarchy and dissimilarity.

The findings of our study unequivocally suggest that the complexity of plant responses to interactions needs a comprehensive set of target traits for conducting interaction experiments. Interestingly, our results can be framed within the postulates of the Modern Coexistence Theory, which conceptualizes coexistence as a delicate balance between mechanisms that stabilize niche differences and those that reduce relative fitness differences (Chesson 2000). In our study, niche differences are represented by trait dissimilarity mechanisms, while relative fitness differences are reflected in trait hierarchy mechanisms. We demonstrate that both forces can operate simultaneously, depending on the trait measured. Translating our experimental findings on the impact of trait variations on species interactions to patterns of species coexistence in natural communities would be a significant step forward in understanding ecological systems and contribute to our knowledge of how diversity in natural communities is maintained.

Author Contributions

Miguel Verdú, Jose Antonio Navarro-Cano, and Marta Goberna designed the experiment. Julia Jimeno-Alda, Jose Antonio Navarro-Cano, and Marta Goberna carried out the experiment and collected the data. Julia Jimeno-Alda and Miguel Verdú performed the

statistical analysis and wrote the first draft, and all authors edited the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data is available on Zenodo online repository at https://doi.org/10.5281/zenodo.14793562.

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Supporting Information

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