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RESEARCH ARTICLE

Transgenerational coexistence history attenuates negative direct interactions and strengthens facilitation

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Abstract

1. Interactions among species are a fundamental aspect of biodiversity and drive ecosystem functioning and services. Species interactions include direct (pairwise) interactions among two species and indirect interactions that occur when a third species interacts and changes the pairwise direct interaction. In a three-species interaction network, these interactions can be transitive (where one species outperforms all others) or intransitive (where each species outperforms another). Here, we investigate how direct and indirect interactions influence ecosystem functions in crop systems and how diversification and evolutionary adaptation can influence those interactions and therefore ecosystem functions.
2. A common garden experiment was conducted with crop communities in monocultures, 2- and 3-species mixtures that had either a common or no coexistence history (i.e. co-adaptation) for the three previous years. Net, direct and indirect interaction intensities were estimated and compared between the diversity levels and coexistence histories. Furthermore, species interaction networks were inspected for transitive/intransitive interactions.
3. We found evidence for less intense competition in mixtures and for reduced negative direct interaction intensity and enhanced facilitative effects upon co-adaptation. We could further show that indirect interactions were generally less important for co-adaptation than direct interactions. Additionally, we showed that co-adaptation has the potential to shift interactions in the species interaction networks from competitive intransitive into pairwise competitive interactions where interactions occurred mainly between two species.
4. *Synthesis.* Co-adapted crop species with reduced negative interactions might have the potential to enhance productivity, especially in more diverse cropping systems. This supports the notion that intercropping is a vital part towards a more sustainable agriculture and one with further yield potential when developing cultivars optimised for growth in mixtures.

KEYWORDS

agriculture, breeding, coexistence history, competition, crops, direct interactions, facilitation, indirect interactions, intransitivity, plant–plant interactions

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1 | INTRODUCTION

Interactions among species are omnipresent. Many of these interactions are competitive, where species compete for certain resources (Levine, 1976). Nevertheless, interactions among species can also be positive (i.e. facilitation) and occur when one species enhances the fitness of another species (Brooker et al., 2008; Hunter & Aarssen, 1988). These (positive and negative) interactions are important for community assembly (Schöb et al., 2013), species coexistence (Levine et al., 2017) and can have evolutionary consequences for the species involved (Thorpe et al., 2011).

In a community with two individuals, the direct interactions between these two individuals are often very intense (Figure 1a). These direct interactions are usually attenuated in communities with more than two individuals (Aschehoug & Callaway, 2015; Levine et al., 2017) due to the presence of indirect interactions which attenuate the competitive effects of the individuals involved in a pairwise interaction (Figure 1b; Callaway, 1997; Miller, 1994). Specific forms of interaction networks involving direct and indirect interactions are intransitive networks (Allesina & Levine, 2011; Gallien et al., 2017), where each species is more competitive than another species in the community (Figure 1c), thereby promoting coexistence. Alternatively, transitive networks show a hierarchical structure in competitive ability (Figure 1d), which tend to result in the most competitive species becoming dominant and the less competitive species being competitively excluded (Hardin, 1960). Hence, direct and indirect interactions and their interaction network have ecological and evolutionary consequences on communities (Lawlor, 1979; Schöb et al., 2013; Strauss, 1991; Wootton, 1994).

In a crop system, the reduction in negative interactions between individuals is essential to mitigate negative effects on fitness or yield

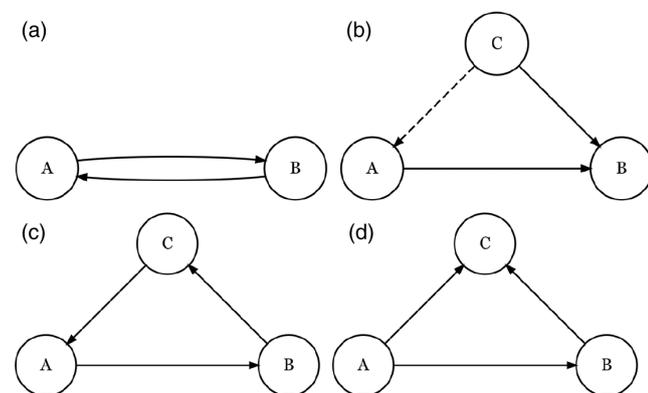


FIGURE 1 Different types of interactions between two or three individuals. (a) Direct (pairwise) interaction with reciprocal negative effects between A and B. (b) Indirect interaction when C interacts with A and B. The original negative interaction from B on A is attenuated (or disintegrated) as C is more competitive against B. Hence, C has a positive indirect effect on A (dashed line). (c) Intransitive interaction between A, B and C where each individual is more competitive than another one ('rock-paper-scissor' game). (d) Transitive ('hierarchical') interaction between A, B and C where A is more competitive than B and C and B more competitive than C.

of the individuals composing the crop community (Donald, 1981; Vandermeer, 1989; Weiner et al., 2017). However, the commercial crop species used nowadays are highly bred which might have selected for high-yielding 'selfish' individuals that intensify competition (Weiner, 2019) rather than promoting cooperative behaviour (Wuest et al., 2022). Hence, studying interactions among crop species helps to understand how species are competing with others in a crop field. Furthermore, breeding of crop species might have reduced phenotypic plasticity (Brooker et al., 2022; Vilela & González-Paleo, 2015), although phenotypic plasticity can help plants to reduce competition (Callaway et al., 2003; Schmutz & Schöb, 2023a). Therefore, breeding crops with reduced competition (or enhanced facilitation) and a more cooperative behaviour is a goal (Wuest et al., 2022). Indeed, studies in natural plant communities have demonstrated that natural selection in diverse communities can reduce competition, increase facilitation and consequently increase ecosystem functioning (Schöb et al., 2018; van Moorsel et al., 2018). Similarly, in an annual crop system, crop communities with a common coexistence history showed decreased competition compared with communities composed of crops that did not share a common history (Stefan et al., 2022). This suggests that evolutionary plant breeding of crops in diverse communities (i.e. mixtures) might select for reduced competition, a more cooperative behaviour and more community-level yield.

While growing crops in species mixtures tends to show reduced competition and higher yields than monoculture due to the simple fact of niche differences between species (Zupinger-Dingley et al., 2014), breeding for mixture ecotypes could unfold an additional yield potential of crop mixtures (Bourke et al., 2021; Moore et al., 2022). Using evolutionary processes in mixtures as a tool for breeding mixture ecotypes seems like an easy and straightforward way towards that aim.

In this study, we aimed to link evolutionary adaptation through a transgenerational coexistence history (i.e. co-adaptation) with direct and indirect interaction intensities within (i.e. intraspecific) and between crop species (i.e. interspecific). We further examined how co-adaptation affects the crop species interaction network. Particularly, the following research questions were addressed: Does co-adaptation change intra- and interspecific net, direct and indirect interaction intensities (question 1)? Are both direct and indirect interactions equally important in co-adaptation (question 2)? How does co-adaptation change the interaction network towards transitivity or intransitivity (question 3)? How does co-adaptation change the relationship between productivity and interaction intensities (question 4)? We hypothesised that co-adaptation decreases negative net and direct interactions (i.e. competition) and increases positive indirect interactions (i.e. facilitation; question 1) and that indirect interactions play an important role in co-adaptation (question 2). Furthermore, we expected that upon co-adaptation interactions in the species interaction network are significantly shifted and that upon co-adaptation interactions are predominantly intransitive (question 3). Lastly, we hypothesised that co-adaptation had a positive effect on community productivity through an attenuated relationship between interaction intensity and productivity (question

4). To test these hypotheses, a common garden experiment was conducted with six different crop species that had either a common coexistence history or no coexistence history. The comparison between communities with or without coexistence history allows to investigate how transgenerational coexistence shapes interactions among plant individuals. Plants were grown in monocultures (i.e. intraspecific interactions) and mixtures (i.e. interspecific interactions), and net, direct and indirect interactions within and between species were calculated and tested for the hypotheses (Figure 2b). Furthermore, species interaction networks with direct and indirect interactions were designed, and the interplay of these interactions was compared.

2 | MATERIALS AND METHODS

2.1 | Establishment of selection histories

The Crop Diversity Experiment in the outdoor experimental garden in Torrejón el Rubio, Cáceres, Spain (39°48'48" N 6°00'01" W) started in 2018 and ended in 2020 (Stefan et al., 2022). In these experiments, originally eight different crop species from four functional groups were grown in different plant diversities, including single plants (i.e. without interaction with other plants) and in 2- and 4-species mixtures (i.e. with interaction with other plants). The initial seed pool originated from local seed suppliers and the gene bank (Stefan et al., 2022). During these 3 years, these crops were grown in rows with the recommended planting densities in plots measuring 0.5 × 0.5 m. The 2- and 4-species mixtures were composed of all possible species combinations among functional groups.

After each cropping season, seeds were collected and resown the subsequent year in the exact same diversity and with the same

species composition and density (Figure 2a). This resulted in two selection histories with plants either having a common coexistence history (i.e. seeds from plants grown in mixtures with a specific species composition, *community* selection history) or no coexistence history (seeds from plants grown as single plant, *single* selection history). In other words, plants from *community* selection history were co-selected and therefore potentially co-adapted, whereas plants which were grown as singles were naïve to other plants.

2.2 | Experimental design

For this study, plants were grown again in the outdoor experimental garden in Torrejón el Rubio, Cáceres, Spain (39°48'48" N 6°00'01" W) from February 2021 until July 2021 in square plots measuring 25 × 25 cm. These plots were arranged in beds of 4 × 40 plots, where the cultures were randomly allocated—except the single plants, which were grown in two separate beds to prevent any above-ground interactions. The beds were irrigated through the whole growing season with an automated irrigation system with thresholds that maintained soil moisture between 50% and 75% of field capacity. To minimise interactions with weeds, plots were regularly weeded. Fertiliser was not applied to the plots. For more detail about the experimental design and the experimental garden (e.g. information about the weather), see Schmutz and Schöb (2023b).

Six different crop species from three functional groups were grown: the cereals oat (*Avena sativa* var. Previsión) and wheat (*Triticum aestivum* var. Cabezorro), the legumes lentil (*Lens culinaris* var. de la Armuña) and lupin (*Lupinus angustifolius* wild type) and the herbs camelina (*Camelina sativa* n.a.) and coriander (*Coriandrum sativum* wild type). These plants were either from *community* or from *single* selection history. Seeds from *community* selection history

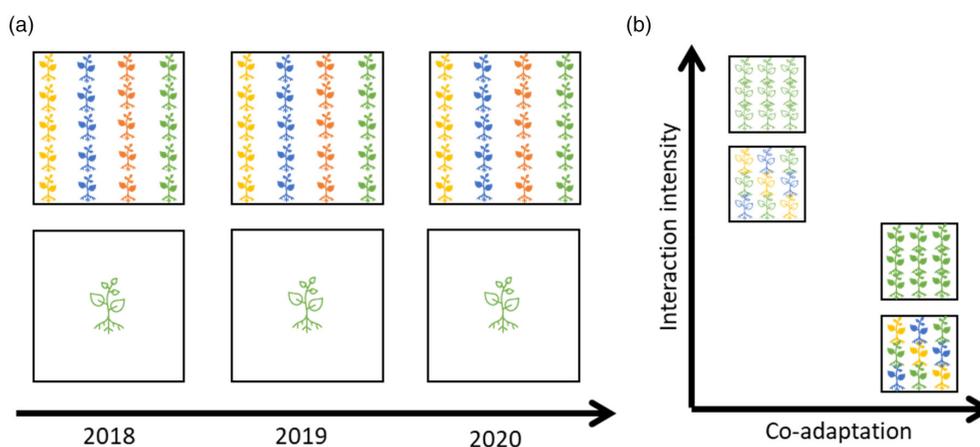


FIGURE 2 Conceptual framework and proposed hypotheses. (a) Establishment of the selection histories previous to this experiment (2018 until 2020). Plants were either grown in mixtures or as single plants for three subsequent years. Seeds from these established selection histories were then used in the subsequent experiment. For simplicity, only a 4-species mixture and a possible single plant are shown. (b) Proposed hypotheses of how co-adaptation (i.e. common vs no coexistence history) among plants affects interaction intensities. Plants from either community or single selection history were grown in plots composing either only one species (intraspecific interactions; monocultures) or multiple species (interspecific interactions; mixtures). (a, b) The shading represents the selection histories (blank = single selection history, filled = community selection history); the colours are different species.

were chosen from mixtures as both intra- and interspecific interactions are present. These species and selection histories were grown as single plant (one individual), in 2×2 (four individuals) and in 3×3 Latin squares (nine individuals; Table 1). The two positions within the 2×2 and the three positions within the 3×3 Latin squares were either occupied by the same species (monocultures) or with other species (mixtures; Figure S1). For the mixtures, all possible combinations between species from the different functional groups were planted together. Within one plot, the plants were either from *community* or from *single* selection history (Table 1). Plants were harvested after complete senescence and seed maturity (starting 7 June 2021). Above-ground biomass was collected for each individual in each plot, and all biomass except seeds was subsequently dried at 80°C for 72 h and weighed.

2.3 | Data analysis

Data analysis was carried out in R version 4.2.0 (R Core Team, 2022). Mean biomass was calculated from the three individuals that occupied the same position within the 3×3 Latin square (Figure S1). Biomass from single plants and 2×2 Latin squares was only used to calculate interaction intensity in the 3×3 Latin squares. Hence, mean biomass in the 2×2 Latin squares was calculated for each species in each species composition and selection history. Along the same vein, mean biomass in the single plants was calculated for each species and selection history.

To calculate interaction intensities, the relative interaction index (RII) was used (Armas et al., 2004). Net interaction intensity (RII_{net}) was calculated for each species in the 3×3 Latin squares. The corresponding biomass when grown as single plant was used as control

(Box 1). Direct ($\text{RII}_{\text{direct}}$) and indirect interaction intensity ($\text{RII}_{\text{indirect}}$) were calculated for each position (a–c) in each 3×3 Latin square plot separately. Direct interaction was calculated from the biomass of the species that received the interaction ('receiver' species) in the 3×3 Latin square and the biomass of the receiver species in the 2×2 Latin square that was lacking the species that imposes the direct interaction ('donor' species) on the receiver species (Box 1; Aschehoug & Callaway, 2015). The indirect interaction was calculated from the product of direct interaction intensities in the 3×3 Latin squares which were mediated by the third species (Box 1, Figure S2b). To prevent pseudoreplication in the monocultures, the mean of direct and indirect interaction among the three positions in each monoculture plot was calculated. The total interaction intensity (RII_{sum}) of the donor species on the receiver species was calculated by the sum of direct and indirect interaction intensities (Box 1).

RII_{net} gives information about the effect of the whole community on a species. On the contrary, $\text{RII}_{\text{direct}}$, $\text{RII}_{\text{indirect}}$ and RII_{sum} are indices of interaction strength of the donor species on the receiver species (i.e. interaction strengths between species pairs). Even though these three interaction intensities always occur between species pairs, they still describe different mechanisms. $\text{RII}_{\text{direct}}$ describes the interaction strength a receiver species experiences with the presence of another (donor) species. On the contrary, $\text{RII}_{\text{indirect}}$ denotes the interaction strength a receiver species perceives from a donor species when (beside the donor species) a third species is present through which this interaction is mediated. Even though $\text{RII}_{\text{indirect}}$ involves a third (mediating) species, the interaction still occurs between a (donor–receiver) species pair. In many cases, indirect interactions counteract or even neutralise direct interactions ('the enemy of my enemy is my friend'). For this reason, the RII_{sum} was estimated, which illustrates the interplay between direct and indirect interactions.

Planting scheme	Culture	Selection history	
		Community	Single
Single plant (1 individual)			
2×2 Latin square (4 individuals)	Monoculture		
	Mixture		
3×3 Latin square (9 individuals)	Monoculture		
	Mixture		

TABLE 1 Overview of the different planting schemes. The shading represents the different selection histories, and the colours are different species.

Subsequently, linear mixed models (LMM) were conducted for the interaction intensities (R packages *lme4* (Bates et al., 2015) and *lmerTest* (Kuznetsova et al., 2017)). For the net interaction intensity, RII_{net} (square-root-transformed) was the response variable; species, culture (monoculture vs mixture), selection history (community vs single) and all possible interactions were the explanatory variables; and the species composition was the random term. For direct, indirect and total interaction intensities, RII_{direct} , $RII_{indirect}$ and RII_{sum} , respectively, were the response variables; the receiver species, the donor species, the selection history and all possible interactions were the explanatory variables; and the species composition was the random term. Type-I analyses of variance (ANOVA) were performed to test the hypotheses. Afterwards, post hoc analyses were conducted to test whether there are significant differences between selection histories and/or culture \times selection history (estimated marginal means, R package *emmeans*; Lenth, 2021). For direct, indirect and total interaction intensities, estimated marginal means of the interaction receiver species \times donor species \times selection history were tested against zero (one-sample t-test). The interaction intensities significantly different from zero were used in the species interaction networks (Figure S2a). Therefore, for the interaction networks, estimated marginal means were used, which represent the means estimated across all species compositions. This method reduced the number of interactions among species and therefore made interpretation easier. However, this method did not allow to calculate saturated interaction networks, as only interactions among species which were actually grown together were estimated.

Intransitivity and transitivity of interactions between three species were defined according to Gallien et al. (2018; Table 2). An additional denotation was introduced to describe interactions that did not include all three species (i.e. pure pairwise). Transitivity/intransitivity was only described on species interaction networks with RII_{sum} (Figure 4c,f).

To test for a relationship between net interaction intensity of a species (estimated marginal means, Figure 3c) and the sum of all direct and indirect interaction intensities a species received from all donor species (estimated marginal means, Figures S3 and S4), a simple linear regression was conducted ($RII_{net} \sim RII_{calc}$).

Community biomass was calculated from communities in the 3×3 Latin squares which had biomass data in all three positions (a–c). A LMM was applied with the square-root-transformed community biomass as response, the selection history as explanatory variable and the species composition as random term. To test for relationships of community biomass with interaction intensities, mean community RII_{net} , RII_{direct} and $RII_{indirect}$ were calculated. In the subsequent LMMs, the community biomass (square-root-transformed) was the response, and RII_{net} , RII_{direct} and $RII_{indirect}$ (community means), respectively, the selection history and the interaction between the interaction intensities and the selection histories were the explanatory variables. The species composition was the random term. A second-degree polynomial function was included when this was significant (which was the case for RII_{direct} and $RII_{indirect}$). Estimated marginal means were used to draw the estimates and the regression lines.

3 | RESULTS

3.1 | Interaction intensities in communities with common and no coexistence history

RII_{net} was significantly less negative in *community* than *single* selection history across all species (Figure 3a, Table 3). Nevertheless, this

BOX 1 Formulas for the calculation of the interaction intensities.

To calculate interaction intensities, the relative interaction index (RII) was used (Armas et al., 2004). All interaction intensities were calculated for each focal individual in all 3×3 Latin squares (here individual A). Direct and indirect interaction intensities were then calculated between the focal individual (receiver individual) and the individual that imposed the interaction (donor individual; here individual B).

The net interaction intensity (RII_{net}) was calculated with the biomass of the focal individual in the 3×3 Latin squares and the biomass of the focal individual as single plant. RII_{net} describes the interaction intensity of the community on a plant in general.

$$RII_{net, A} = \frac{(B_{A,ABC} - B_{A,single})}{(B_{A,ABC} + B_{A,single})} \quad (1)$$

The direct interaction intensity (RII_{direct}) was calculated with the biomass of the receiver individual in the 3×3 Latin squares and the biomass of the receiver individual in the 2×2 Latin squares where the donor individual was lacking. RII_{direct} describes the interaction strength the receiver individual receives from the presence of another (donor) individual.

$$RII_{direct, A \text{ from } B} = \frac{(B_{A,ABC} - B_{A,AC})}{(B_{A,ABC} + B_{A,AC})} \quad (2)$$

The indirect interaction intensity ($RII_{indirect}$) was calculated from the product of direct interaction intensities in the 3×3 Latin squares which were mediated by the third individual (here individual C; Figure S2b). $RII_{indirect}$ describes the interaction strength a receiver individual receives from a donor individual when another third (mediating) individual is present which mediates the interaction.

$$RII_{indirect, A \text{ from } B} = RII_{direct, C \text{ from } B} * RII_{direct, A \text{ from } C} \quad (3)$$

The total interaction intensity (RII_{sum}) was calculated from the sum of direct and indirect interaction intensities the receiver individual received from the donor individual. RII_{sum} facilitates the interpretation of the interplay between RII_{direct} and $RII_{indirect}$.

$$RII_{sum, A \text{ from } B} = RII_{direct, A \text{ from } B} + RII_{indirect, A \text{ from } B} \quad (4)$$

effect was only significant in mixtures whereas in monocultures the same, but weaker (not significant) trend was visible (Figure 3b). Especially oat, lentil and lupin in mixtures and coriander from

TABLE 2 Interaction denotations used in this study. Pure pairwise interaction occurs when only two out of the three species were involved in the interactions or when the interaction between three species could not be denoted as transitive, intransitive or a form between the two (weak intransitive). Transitive interactions are hierarchical where one species outperforms the two and one species is the least competitive whereas intransitive interactions occur when each species outperforms another species.

Denotation of interaction	Interactions
Pure pairwise	$A > B, A > C, B > C$
Transitive ('hierarchical')	$A > B > C$ and $B > C$
Weak intransitive	$A > B > C = A$
Intransitive ('rock-paper-scissor')	$A > B > C > A$

monoculture plots experienced a less negative RII_{net} in *community* selection history (Figure 3c). For camelina from mixture plots, RII_{net} was significantly but only slightly less negative in *single* than *community* selection history. In general, for most plants, RII_{net} was negative and very strong. Only lupin grown in mixture experienced facilitative effects—these positive effects were even more pronounced in *community* selection history. The culture alone had a large impact, especially on RII_{net} of lupin, camelina and coriander (Figure 3c). This indicates that intra- and interspecific interactions had varying effect on species RII_{net} .

Both RII_{direct} and $RII_{indirect}$ were affected by selection history, but the effect depended on the receiver and donor species (Table 3). Subsequent post hoc analyses revealed that in most cases, negative RII_{direct} was reduced in *community* selection history (Figure S3). In the two cereals, oat and wheat, the selection history had no effect on interaction intensity. The receiver species lentil and lupin always showed reduced negative RII_{direct} (i.e. competition) in *community*

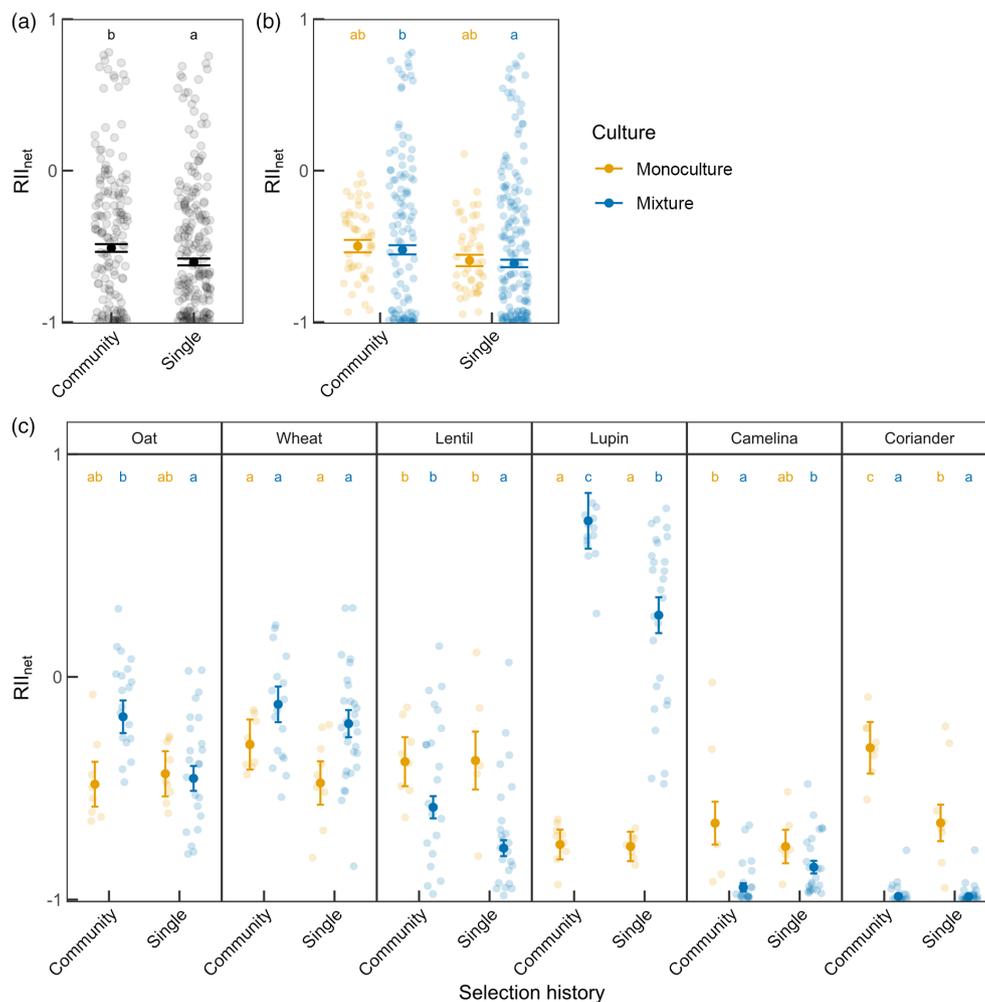


FIGURE 3 Net interaction intensity (RII_{net}) of plants with either *community* or *single* selection history. (a) RII_{net} across all species but separately for selection history. Shown are the single data points, the estimated marginal means \pm standard error and the grouping according to the contrast analysis of selection history. (b) RII_{net} across all species from the two selection histories and grown either in monocultures (yellow) or mixtures (blue). Shown are the single data points, the estimated marginal means \pm standard error and the grouping according to the contrast analysis of culture \times selection history. (c) RII_{net} of the six species from the two selection histories and grown either in monocultures (yellow) or mixtures (blue). Shown are the single data points, the estimated marginal means \pm standard error and the grouping according to the contrast analysis of culture \times selection history within each species separately.

selection history. In camelina, this trend depended strongly on the donor species. For $RII_{indirect}$, significant differences between selection histories were only present in lentil and camelina—and also only imposed by the donor species oat and wheat (Figure S4). In all these cases, *single* selection history showed increased positive $RII_{indirect}$ (i.e. indirect facilitation).

RII_{sum} (sum of direct and indirect interactions) showed a similar pattern like RII_{direct} (Figure S5, Table 3). In some cases, the $RII_{indirect}$ counteracted the effect of selection history on RII_{direct} (e.g. in receiver-donor pairs lentil–wheat and camelina–camelina). In other cases, $RII_{indirect}$ enhanced selection history effects on RII_{direct} . These include the receiver–donor pairs camelina–wheat, coriander–lentil and coriander–lupin. In all these cases, $RII_{indirect}$ especially reduced negative direct interactions in *single* selection history. In fact, RII_{direct} and $RII_{indirect}$ showed a weak but significant negative relationship (Figure S6a).

3.2 | Species interaction networks

The number of significant intraspecific direct interactions was largely affected by selection history (Figure 4a,d). Direct interactions were generally fewer in *community* than in *single* selection history. In *community* selection history, coriander and camelina received most of the (negative) direct interactions—oat, wheat and lupin were the species that imposed most of the interactions (Figure 4a). In comparison with *community* selection history, it was additionally lentil in the *single* selection history that received several negative direct interactions (Figure 4d). Moreover, in *single* selection history, oat was also more frequently involved in receiving and imposing negative direct interactions. Reciprocal negative interactions that were present in *single* selection history do not appear in *community* selection history (e.g. in oat–lentil, lentil–camelina and wheat–lupin). Contrary to intraspecific direct interactions, the number of interspecific direct interactions was generally less affected by selection history.

Significant indirect interactions were generally fewer than direct interactions, always positive and had a similar extent in both selection histories (Figure 4b,e). Positive indirect interactions especially in monocultures seemed very effective in mitigating negative direct interactions. In all monocultures and both selection histories, previously negative direct interactions were mitigated by indirect interactions (Figure 4c,f). Other than that (especially in intraspecific interactions), indirect interactions could not counteract the strong negative direct interactions. This can mainly be explained by the presence of stronger negative direct interactions between species than within species.

Intransitivity and transitivity of interactions were greatly influenced by selection history (Figure 4c,f, Table S1). In *community* selection history, from all the possible interactions between three species, most interactions were pure pairwise (e.g. oat>lentil, lupin>camelina; Table S1). There was only one weak intransitive interaction present between oat, lentil and coriander (i.e. oat>lentil>coriander=oat). In contrast, interactions in *single* selection history were mostly weakly

intransitive. Additionally, two transitive interactions were also present in *single* selection history (i.e. lupin>oat>camelina and lupin>camelina, wheat>coriander>lentil and wheat>coriander; Table S1).

3.3 | Community productivity and its relationship to the interaction intensities

Community productivity was 26% higher in *community* than in *single* selection history (Figure 5a, Table S2). Furthermore, community productivity and the different interaction intensities (community means) were generally related—but the relationship varied between interaction intensities (Figure 5). RII_{net} and community productivity showed a positive relationship (Figure 5b), with slightly different slopes among selection histories (Table S2). The relationship between community productivity and both RII_{direct} and $RII_{indirect}$ was best described by a second-degree polynomial function (Table S2). There was no significant difference in these relationships between selection histories—neither for the linear nor for the quadratic term (Table S2). Community productivity and RII_{direct} showed a positive relationship with negative RII_{direct} values, followed by a community productivity maximum (turning point) at RII_{direct} values around zero (Figure 5c). In other words, communities were most productive when RII_{direct} was neutral (neither positive nor negative). On the contrary, the relationship among community productivity and $RII_{indirect}$ showed a negative relationship (Figure 5d). This indicates that less productive communities had more positive $RII_{indirect}$. In summary, the most productive communities had low RII_{net} , RII_{direct} around zero and neutral $RII_{indirect}$.

4 | DISCUSSION

With the method applied here to estimate direct and indirect interaction intensities between plants, we were able to study how co-adaptation affects these interactions in an agricultural system. We found that co-adaptation reduced overall competition and negative direct interactions between species, especially in more diverse plant communities. Co-adaptation had a substantial impact on the interplay in the species interaction network and reduced mainly the number of direct interactions among plants in the community. Furthermore, co-adapted communities were generally more productive than naïve communities, which was directly related to the less negative interaction intensities experienced in co-adapted communities (Figure 5).

4.1 | The importance of direct and indirect interactions in co-adaptation

In this study, we found evidence for reduced competition after co-adaptation of species in a community (Figure 3a). This finding

TABLE 3 Type-I analysis of variance from the linear mixed effect models of net (RII_{net}), direct (RII_{direct}), indirect ($RII_{indirect}$) and total interaction intensity (RII_{sum}). For RII_{net} , the explanatory variables were species, culture, selection history and all possible interactions between the three variables. For the others (RII_{direct} , $RII_{indirect}$ and RII_{sum}), the explanatory variables were receiver species, donor species, selection history and all possible interactions between the three variables. The random term was species composition. DF, degrees of freedom; DenDF, degrees of freedom of error term; F, probability distribution; p, error probability. p-values in bold are significant at $\alpha=0.05$.

	df	DenDF	F	p
RII_{net}				
Species	5	42.61	141.90	<0.001
Culture	1	7.55	0.00	0.972
Selection history	1	332.48	12.54	<0.001
Species × culture	5	13.17	47.93	<0.001
Species × selection history	5	328.66	3.92	0.002
Culture × selection history	1	329.72	0.02	0.882
Species × culture × selection history	5	326.54	4.57	<0.001
RII_{direct}				
Receiver species	5	53.15	18.09	<0.001
Donor species	5	67.67	7.34	<0.001
Selection history	1	448.64	2.40	0.12
Receiver species × donor species	19	59.17	1.52	0.111
Receiver species × selection history	5	558.62	5.29	<0.001
Donor species × selection history	5	558.19	1.58	0.164
Receiver species × donor species × selection history	19	557.51	3.78	<0.001
$RII_{indirect}$				
Receiver species	5	46.42	4.56	0.002
Donor species	5	57.82	3.87	0.004
Selection history	1	426.46	0.86	0.354
Receiver species × donor species	19	46.61	2.46	0.006
Receiver species × selection history	5	545.88	1.53	0.178
Donor species × selection history	5	545.44	1.32	0.252
Receiver species × donor species × selection history	19	544.58	1.76	0.025
RII_{sum}				
Receiver species	5	55.39	9.98	<0.001
Donor species	5	46.08	3.11	0.017
Selection history	1	467.94	0.95	0.330
Receiver species × donor species	19	30.42	3.06	0.003
Receiver species × selection history	5	543.21	8.00	<0.001
Donor species × selection history	5	543.10	1.64	0.147
Receiver species × donor species × selection history	19	542.84	6.81	<0.001

is in line with a study that also found reduced competition in communities with a common coexistence history (Stefan et al., 2022). Furthermore, co-adaptation reduced competition particularly between species (i.e. interspecific interactions) whereas competition within a species (i.e. intraspecific interactions) was not affected (Figure 3b). Additionally, facilitative effects of the community on lupin were only present in mixtures and more pronounced upon co-adaptation (Figure 3c). This confirms that species diversity is crucial for the evolution of facilitation among plant species (Schöb et al., 2018). Besides, species diversity is also suggested to enhance indirect interactions and mitigate negative interactions

(Aschehoug & Callaway, 2015). The net effects of the community on the species were also reflected in the direct and indirect interactions the species received. In fact, the sum of direct and indirect interaction intensities (as quantified with RII in our study) was a good predictor of the net effects (Figure S6b). This suggests that RII is a suitable measure to partition net effects into direct and indirect interactions.

In our system, direct interactions were strong and always negative, which implies strong competition among the crop species. This can probably be explained by the high plant density within the small plots. Furthermore, direct interactions were calculated with

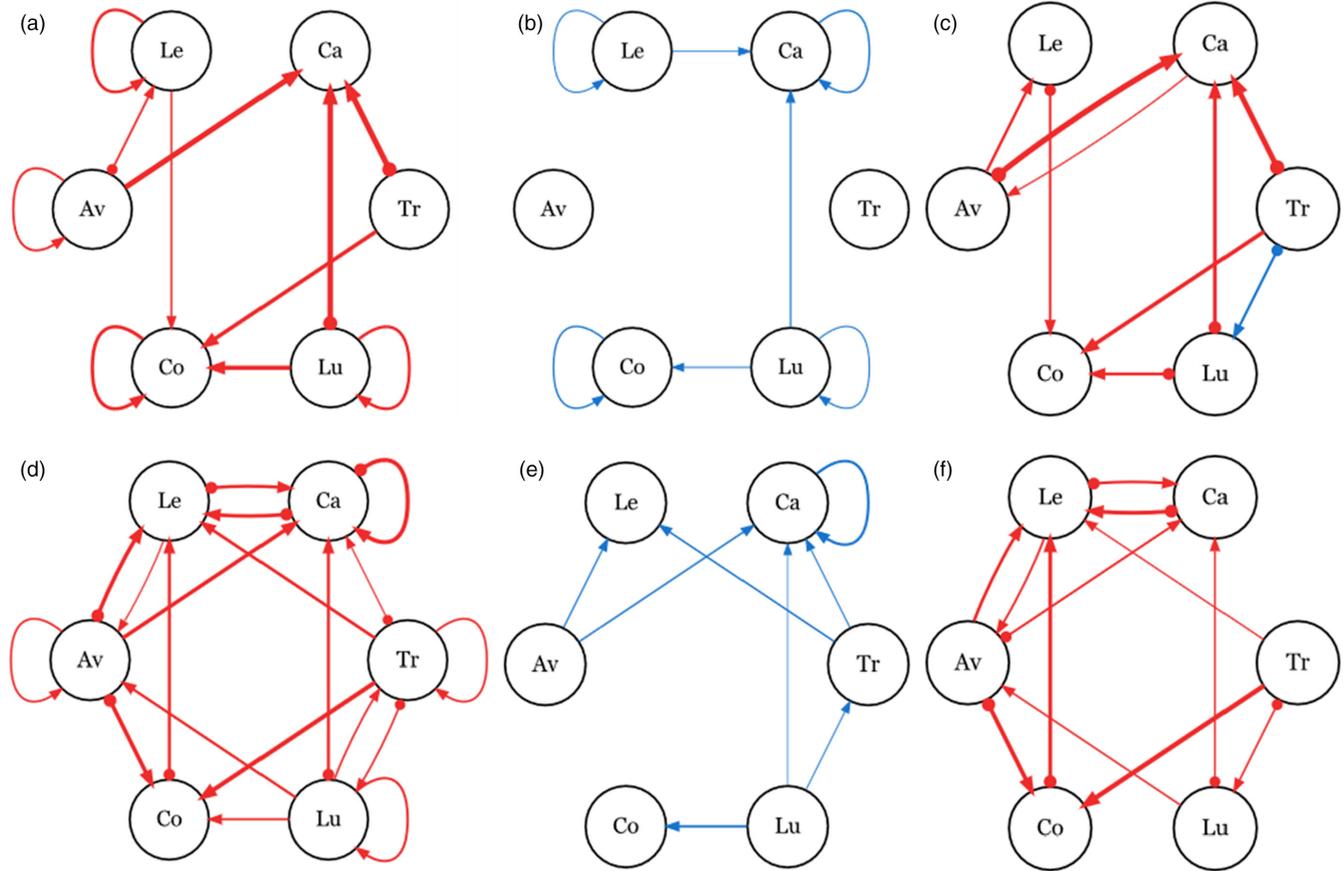


FIGURE 4 Interaction networks in the communities. Direct (RII_{direct}) (a, d), indirect (RII_{indirect}) (b, e) and total interactions (RII_{sum}) (c, f) in communities that consisted of plants with either *community* (a–c) or *single* selection history (d–f). Blue arrows represent positive, red negative interactions. Shown are only the interaction intensities (estimated marginal means) that were significantly different from zero. Significant differences between the selection histories are indicated with a dot on the arrow tail (compared with S3–S5). Arrow thickness corresponds to the interaction intensity (stronger positive or negative interaction intensities are thicker). Species abbreviations correspond to Av = oat, Tr = wheat, Le = lentil, Lu = lupin, Ca = camelina and Co = coriander.

the plant biomass in 3×3 Latin squares (nine individuals) and with the plant biomass in 2×2 Latin squares (four individuals) as control. The additional species (which imposed the direct interaction) in the 3×3 Latin squares was always accompanied by a higher plant density. Consequently, significant direct interactions were exclusively negative, as expected (Miller, 1994; Vandermeer, 1990).

In addition to co-adaptation significantly reducing competitive effects in the community (Figure 3), it also decreased the intensity and number of negative direct interactions (Figure S3, Figure 4a,d). As far as we know, this is the first study that has demonstrated a positive effect of community adaption on competitive direct interactions. Nevertheless, direct interactions were generally more dominant than indirect interactions and the indirect facilitative effects could not counteract the strong direct competitive effects (Figure 4). Consequently, indirect interactions were rather insignificant for co-adaptation in our study system. There is both theoretical (Lawlor, 1979; Levine et al., 2017) and empirical evidence (Cuesta et al., 2010; Michalet et al., 2015; Schöb et al., 2013) that underpins the importance of indirect interactions for plant coexistence and community structure. Additionally, indirect interactions

are suggested to have evolutionary consequences on communities (Guimarães et al., 2017; Wootton, 1994). Yet, empirical evidence about the importance of indirect interaction for adaptation of plants in plant communities is lacking. This might be due to the fact that indirect interactions are generally hard to measure as they are not as apparent as direct interactions (Strauss, 1991).

4.2 | The effect of co-adaptation on transitive and intransitive interactions

In a three-species interaction network, transitive interactions occur when one species is more competitive than the other two and one is the least competitive ($A > B > C$ and $B > C$, Figure 1d, Table 2). On the contrary, intransitive interactions between three species arise when each species is more competitive than one of the others ($A > B > C > A$, Figure 1c, Table 2). However, 'strong' intransitive interactions are hardly found in nature (Soliveres & Allan, 2018). Thus, it was suggested that weak forms of intransitivity can also occur ('weak' intransitive interaction, $A > B > C = A$, Table 2; Gallien

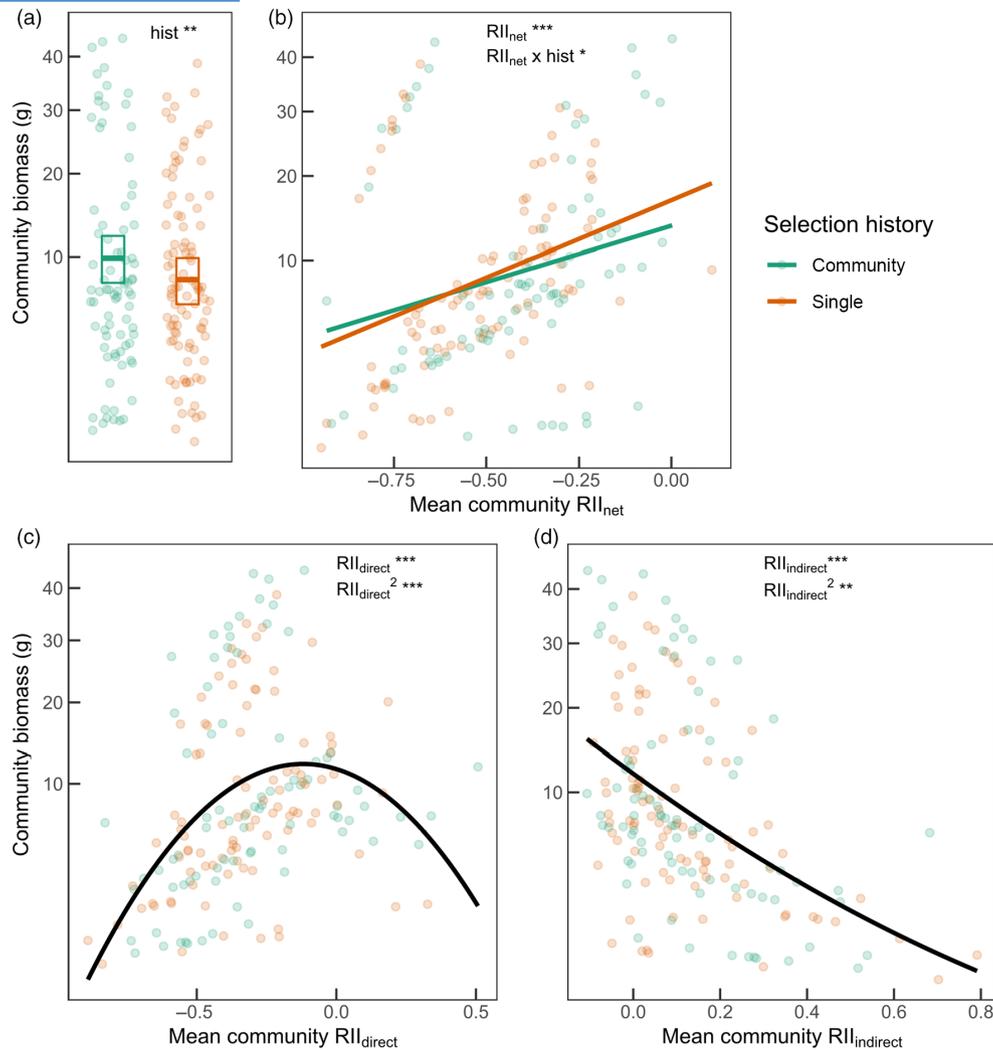


FIGURE 5 Community biomass and its relationship with different interaction intensities (community means). (a) Community biomass separated by selection history. (b) The linear relationship between community biomass and the net interaction intensity (RII_{net}) separated by selection history. (c) The quadratic relationship between community biomass and the direct interaction intensity (RII_{direct}). (d) The quadratic relationship between community biomass and the indirect interaction intensity ($RII_{indirect}$). (a–d) Shown are the single data points and the estimated marginal means (crossbars and regression lines). Significant effects according to the linear mixed models are indicated with asterisk (hist, selection history).

et al., 2018). In our system, co-adaptation reduced the number of (weak) intransitive interactions (Table S1). In most cases, these weak intransitive interactions were diminished to pure pairwise interactions where some species (mostly wheat, lupin and partly oat) were more competitive than other species (mostly lentil, camelina and coriander). Furthermore, transitive interactions were only present in communities without coexistence history (e.g. lupin>oat>camelina and lupin>camelina). Upon co-adaptation, hierarchical negative interactions were diminished to pure pairwise interactions.

Intransitive interactions are also affected by the heterogeneity of the environment (Allesina & Levine, 2011). In less fertile and drier environments, intransitive interactions are more common (Soliveres et al., 2015, 2018). This has large implications for cropping systems, which are usually highly productive (e.g. high fertiliser and water inputs) and very homogeneous. Under these conditions, intransitive

interactions are less likely to exist and evolve (Gallien et al., 2018; Soliveres et al., 2018).

Intransitive competition can certainly be important among interacting crop species (i.e. in intercropping) as it reduces competitive differences among species (Gallien et al., 2017). However, an intransitive interaction that is very competitive probably also does not promote community productivity, which is the main goal in agricultural systems. Thus, the breeding of cooperative plants is essential to enhance agricultural productivity (Weiner, 2019; Weiner et al., 2017; Wuest et al., 2022). In our system, co-adaptation increased competitive ability especially in lupin grown in mixture—and competitive ability of others such as camelina and coriander in mixtures decreased. Consequently, co-adaptation did not promote cooperativeness of the crops, but rather resulted in an imbalance of competitive ability among species (i.e. asymmetric competition,

Weiner, 1990). Nevertheless, this does not imply that community productivity is lower upon co-adaptation.

4.3 | Community productivity upon co-adaptation

Co-adaptation of plants had a positive effect on community productivity, resulting in 26% more biomass in co-adapted communities (Figure 5a). These findings are in accordance with another study, which also showed that co-adapted communities are more productive than naïve communities (van Moorsel et al., 2018). This positive effect of co-adaptation on ecosystem functioning might be relevant for crop production to enhance productivity sustainably.

However, it is important to mention that the planting density applied in this study does not actually match the recommended cultivation practices. Recommended densities are for legumes 160 seeds/m², for cereals 400 seeds/m², for coriander 240 seeds/m² and for camelina 592 seeds/m² (Stefan et al., 2022), while we applied planting densities of 144 plants/m² in the 3×3 Latin squares and even lower in the 2×2 Latin squares. Consequently, interaction intensities could be even more intense when applying the recommended planting densities in a crop field.

In this study, high community productivity was associated with low net interactions (i.e. reduced competition; Figure 5b). This association was slightly stronger (i.e. steeper slope) in naïve communities than co-adapted communities. This suggests that co-adapted communities are also more productive when competition is very intense, which in turn might be interesting in cropping systems where planting densities are high (as discussed above).

Even though the relationship of community productivity with direct and indirect interaction intensities was not affected by co-adaptation (Figure 5c,d), they might still be interesting for crop production. Interestingly, most productive communities were found where direct interactions were neutral and not positive, as might be expected. This implies that communities which include very competitive and less competitive plants (i.e. strong and weak direct interactions) are still more productive than communities which include only plants with low competitive ability. As competitive ability was either enhanced or reduced upon co-adaptation (as discussed above), it offers another explanation for the higher productivity of co-adapted plant communities. Surprisingly, neutral indirect interactions seem to have been associated with more productive communities and communities that showed facilitative indirect interactions were much less productive. In other words, for productive communities, indirect interactions seem less important—and also upon co-adaptation, indirect interactions were not affected.

4.4 | Possible underlying mechanism

Recent research suggests that diverse communities (i.e. mixtures) can impose selection pressures which might affect phenotypes

(Zupping-Dingley et al., 2014), either through genetic or epigenetic changes (van Moorsel et al., 2019). However, maternal effects (i.e. seed size) can also be important for phenotypic plasticity, especially in adaptation to local conditions (Galloway, 2005). These maternal effects, but especially their effect on phenotypic plasticity, might be important when breeding for mixture ecotypes (Brooker et al., 2022; Milla et al., 2017). In fact, mass per seed data from the previous years of the Crop Diversity Experiment indeed suggest that maternal effects cannot be excluded as possible mechanism of the observed patterns—at least for camelina and coriander (Figure S7).

Even though we have no genomic data from the species and selection histories used in this experiment, genetic changes cannot be excluded either. As shown by van Moorsel et al. (2019), the observed phenotypic differences between selection histories (monocultures vs mixtures) in grassland species were mainly due to genetic differences, which suggests that species can evolve rapidly to their biotic environment (i.e. interacting plants; van Moorsel et al., 2019). These evolutionary changes due to adaptation can, among others, occur through (natural) selection or random genetic drift (Wilson & Bossert, 1971). During the establishment of the selection histories used in the experiment described here, seeds were collected and (randomly) resown in the subsequent year. Therefore, both selection and genetic drift could have occurred. It would be interesting to investigate whether and how genetic and/or epigenetic changes shaped the observed phenotypes from the two selection histories (sensu van Moorsel et al., 2019), especially since this has not been done in cropping systems.

4.5 | Conclusion

In this study, we investigated how co-adaptation of crop species affects net, direct and indirect interaction intensities and how transitivity and intransitivity of interactions were shifted upon co-adaptation. We demonstrated that competitive net and direct interaction intensities were mitigated upon co-adaptation. Even though indirect interactions were generally facilitative, they could not counteract the strong competitive direct effects in our system. Facilitation was only found in lupin grown in mixtures and was also more pronounced upon co-adaptation. Moreover, we observed that co-adaptation diminished (weak) intransitive interactions to pure pairwise competitive interactions. Last but not least, we found that co-adaptation enhanced community biomass and that the most productive communities had neutral direct and indirect interactions.

AUTHOR CONTRIBUTIONS

Anja Schmutz planned and conducted the experiment, analysed the data and wrote the manuscript. Christian Schöb obtained funding, planned the experiment and gave advice during the experiment, analysis and manuscript writing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14241>.

DATA AVAILABILITY STATEMENT

The data used in this study are available on Zenodo: <https://doi.org/10.5281/zenodo.7621220> (Schmutz & Schöb, 2023c).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Examples of the planting schemes 2×2 Latin squares and 3×3 Latin squares.

Figure S2. (a) All possible (direct and/or indirect) interactions in this study. (b) Example of the calculation of indirect interactions.

Figure S3. Direct interaction intensity (RII_{direct}) between receiver (interaction to) and donor species (interaction from) of plants with either *community* or *single* selection history.

Figure S4. Indirect interaction intensity ($RII_{indirect}$) between receiver (interaction to) and donor species (interaction from) of plants with either *community* or *single* selection history.

Figure S5. Total interaction intensity (RII_{sum} , sum of direct and indirect interaction intensities) between receiver (interaction to) and donor species (interaction from) of plants with either *community* or *single* selection history.

Figure S6. Relationship between different estimated interaction intensities (estimated marginal means).

Figure S7. Mass per seed (g) of species from *community* or *single* selection history.

Table S1. Interaction denotations across all species compositions and for *community* and *single* selection history for total interaction intensity in Figure 3c,f.

Table S2. Type-I analysis of variance from the linear mixed effect models of community biomass.

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