Intercropping functionally similar species reduces yield losses due to herbivory. A meta-analytical approach

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ABSTRACT

Agroecosystem diversification is often implemented to diminish herbivory and reduce yield losses. However, increasing plant richness does not always reduce herbivory levels, so there is a need for better understanding which polyculture characteristics are effective in deterring herbivores. Here, we evaluated the hypothesis that functional and phylogenetic distances between intercropped species reduce herbivory pressure and enhance natural enemy response. Diminishing herbivory would be brought about by the complementarity and synergy of traits that deter herbivores and benefit herbivore natural enemies, and as a result of a decrease in the availability of host plants for specialized herbivores. Using a meta-analytical approach, we observed lower herbivore abundance and herbivory damage in focal plants when they grew in polycultures. In addition, polycultures showed increased levels of herbivore parasitism and greater abundance of predators and parasitoids, although the effect of the latter two was negligible. Interestingly, the functional distance between crops affected herbivore abundance and herbivory damage in opposite ways, but had no effect on herbivore natural enemy response. Contrary to our expectations, neither herbivory pressure nor natural enemy response appeared to be influenced by phylogenetic distance between intercropped species. Overall, our study provides valuable insights for agroecosystem design aimed at reducing yield loss by strategically intercropping functionally similar species.

1. Introduction

One of the main consequences of agroecosystem simplification and homogenization is an increase in yield losses due to herbivore pests (Oerke and Dehne, 2004; Tamburini et al., 2020). Annually, 26–40 % of yields are lost due to pests in six of the most important crops worldwide (i.e., wheat, rice, maize, potatoes, soybeans and cotton), and modern agriculture invests more than US$30 billion in external inputs to combat pest attacks (Oerke, 2006). However, careful design and management of crop systems can mitigate the economic and ecological impact of herbivory on crop production. Increasing plant richness by arranging crops in polycultures promotes multiple ecological services; for example, increased resource use efficiency, greater availability of suitable habitats for beneficial insects, and natural suppression of insect pests (Huss et al., 2022; Kirsch et al., 2023). Polycultures may decrease the vulnerability of a focal crop to herbivory through associational resistance conferred by heterospecific neighboring plants (Barbosa et al., 2009); and through boosting top-down control (i.e., herbivore predation or parasitism) enhanced by the provision of food and shelter resources for herbivore predators and parasitoids (Haddad et al., 2009; Mitchell et al., 2016).

Several studies have shown the advantages of polycultures over monocultures in suppressing herbivory and enhancing top-down control (e.g., Iverson et al., 2014; Letourneau et al., 2011; Zhang et al., 2017). However, increasing plant richness may not always be positively correlated with herbivory reduction, nor with improvements in other ecological functions (Cadotte et al., 2011; Poveda et al., 2008; Singh et al., 2017). In some cases, diversified agroecosystems have even increased the vulnerability of focal crops to herbivory (Huss et al., 2022). This demonstrates that not all polyculture configurations

effectively reduce yield losses caused by herbivory. There is therefore a need for more comprehensive research to determine which specific polyculture characteristics are effective in preventing yield losses. Accordingly, there has been a steady increase in research on the functional traits and phylogenetic history of plants, and herbivores and their natural enemies in an attempt to understand how diversity promotes herbivory reduction in productive habitats (e.g., Coco et al., 2022; Greenop et al., 2018; Hahn and Cammarano, 2023; Loranger et al., 2013).

Plants have developed a great diversity of functional traits involved in resistance to herbivory, and these vary among plant species (Futuyma and Agrawal, 2009). However, plant domestication has led to a reduction in defensive trait production, which results in an increase in crop susceptibility to herbivore attacks (Fernandez et al., 2021; Rosenthal and Dirzo, 1997; Whitehead et al., 2017). Nevertheless, focal crop species intercropped with others frequently suffer less herbivore damage than plants growing in monocultures (e.g., Maluleke et al., 2005; Sekamatte et al., 2003). First, the presence of non-host neighbors can hinder the localization of host plants by herbivores (Castagneyrol et al., 2013). Also, plants growing in heterospecific patches can be of mutual benefit through the production of repellent or antifeedant compounds that negatively influence herbivore abundance (Barbosa et al., 2009), and through the release of VOCs (i.e., volatile organic compounds) that warn nearby plants of herbivore presence (Kessler et al., 2006). Finally, heterospecific neighbors can favor the presence of herbivore predators and parasitoids through the release of attractive chemical cues and the provision of nutritional (e.g., nectar, food bodies) and shelter resources (Hernandez et al., 2013; Jones et al., 2017; Landis et al., 2000; Mockford et al., 2022).

Functional distance between species indicates ecological dissimilarities or trait diversity (Díaz and Cabido, 2001), and is often positively correlated with ecosystem functionality (Cadotte et al., 2011; Díaz et al., 2006). Therefore, plant species with very dissimilar defensive traits are separated by a high functional distance, and this may impact directly on herbivory reduction in polycultures. Increasing functional distance may increase synergy and/or complementarity between direct defensive traits that deter herbivores, and between indirect defensive traits that benefit herbivore natural enemies (Barbosa et al., 2009; Landis et al., 2000). Likewise, herbivores specializing in a particular focal plant may not be able to use functionally dissimilar plants, so herbivore load may decrease when functional distance increases (Root, 1973). Thus, we hypothesized that polycultures with a high functional distance between co-existing crop species will promote herbivory reduction through bottom-up and top-down mechanisms led by direct defensive traits and herbivore natural enemies, respectively. However, given that other plant traits such as growth rate, morphology or phenology can also influence plant vulnerability to herbivores (Carmona et al., 2011; Loranger et al., 2013), defensive trait dissimilarities may not be enough to explain or predict polyculture resistance.

Due to the evolutionary conservatism of many functional traits, phylogenetically close species are expected to have similar niches, including ecological interactions (Aizen et al., 2016; Gilbert and Webb, 2007; Gómez et al., 2010). Particularly, phylogenetically related species often share herbivore assemblages, and when grown together this can increase the susceptibility of a focal plant to herbivory (Pearse and Hipp, 2009; Yguel et al., 2011). High phylogenetic and functional distance may promote herbivory reduction by similar mechanisms: the synergy or complementarity of plant traits that discourage herbivore attacks or benefit herbivore natural enemies, and a reduction in resource availability for specialized herbivores (Srivastava et al., 2012). However, the phylogenetic distance between species involves a wider range of ecological traits than does functional distance, and therefore it is usually a better predictor of ecosystem functionality (Flynn et al., 2011; Yguel et al., 2011). Therefore, when plant traits influencing herbivory and herbivore natural enemies' attraction are evolutionary conserved, we expect phylogenetic distance between plants to influence levels of herbivory and natural enemy response in polycultures.

In a comprehensive meta-analysis, Barbosa et al. (2009) observed that a neighbor's palatability and phylogenetic proximity influenced herbivore abundance and damage in focal plants. Since palatability is defined by nutritional quality and anti-herbivore defenses, Barbosa et al. (2009) highlighted the importance of defensive traits in the herbivory resistance imparted by plant diversity. In this study, we examined how variation in direct defensive mechanisms among intercropped plants affected herbivore pressure. We also explored how the dissimilarity of plant resources available to herbivores' natural enemies, such as extra-floral nectar and volatile organic compounds (VOCs) (i.e., indirect defensive traits), influence the abundance of predators and parasitoids and their attacks on herbivores. Furthermore, to complement the functional trait approach, we evaluated the influence of the phylogenetic dissimilarity between intercropped plants in reducing herbivory and enhancing the natural enemy response. Lastly, we evaluated the relation between the functional (focusing on direct and indirect defensive traits) and phylogenetic distances between crops. Considering ancestral trait conservatism, we expected positive correlations between the two distance measures. We applied a meta-analytical approach that allowed us to explore the mechanisms more comprehensively and to capture global patterns across different polyculture species compositions, focal crops, management strategies, and geographic regions. Also, the inclusion of polycultures containing different plant species combinations enabled us to cover a larger gradient of functional and phylogenetic distances than would have been possible with an experimental approach.

2. Methods

2.1. Database

We constructed two separate databases, one for herbivory pressure and the other for the natural enemy response. We extracted information from published articles reporting any measurement of herbivore abundance, herbivory damage, natural enemy abundance or natural enemy pressure on herbivores; we included data proceeding from mono- and polycultures cultivated under similar conditions (e.g., supply applications, plot scale, sowing date) to preclude confounding effects from external factors. We carried out the bibliographic search in Google Scholar during 2020 and 2021, using the following term combinations: "polyculture", "monoculture", "ecosystem services", "herbivory", "herbivory damage", "natural enemy control", "predators", "parasitoids"; "mixed cropping", "intercropping", "herbivory", "herbivory damage", "natural enemy control"; "polyculture", "monoculture", "ecosystem services", "herbivore", "pest control", and "tritrophic control". To complement this search, we examined the studies included in three previous meta-analyses (i.e., Barbosa et al., 2009; Iverson et al., 2014; Letourneau et al., 2011). We restricted the inclusion of data to sources that described the species composition of mono- and polycultures and reported all the estimates needed for a classical meta-analysis. We considered as polycultures those systems in which two or more plant species coexisted in time and space within a plot. Monocultures were always sown with commercial species, but some polycultures included both commercial and non-commercial species. Herbivory pressure was scored through measurements of herbivore abundance on focal species or per plot (hereafter "herbivore abundance") and plant percentage consumed or damaged in focal species (hereafter "herbivory damage") (Table S1). Herbivore natural enemy measurements included predator abundance, parasitoid abundance, and number or percentage of parasitized herbivores (hereafter "herbivore parasitism"; Table S2). From tables and graphs we extracted mean values, sample sizes and variance estimations for monocultures and polycultures, using the free software ImageJ (https://imagej.nih.gov/ij/download.html). Most of the studies reported multiple measurements of the assessed variables, and some reported measurements repeated in time for multiple polycultures and monocultures. We extracted the multiple measurements reported;

however, non-independent records were summarized in a single effect size (see Section 2.3 *Effect size*).

We calculated the functional and phylogenetic distances between species in polycultures. The functional distances represented the degree of dissimilarity of functional traits between species (Díaz and Cabido, 2001) within polycultures: the chemical and physical direct defensive traits for the herbivory database, and indirect defensive traits (i.e., floral resources, VOCs) for the natural enemy database. To calculate the functional distances, we characterized each plant species according to type of direct defensive trait (e.g., terpenoids and trichomes) and the traits involved in herbivore natural enemy attraction (i.e., indirect defensive traits; Supp. mat. N1, Tables S3). For each pair of species, we then calculated the Jaccard dissimilarity index (Greenacre and Primicerio, 2013; Legendre and Legendre, 1998) for direct and indirect defensive traits, separately and pooled (Tables S4-S6). Because the studies included in our databases did not report functional traits, we performed a separate bibliographic search for these traits; we chose not to include trait abundance, when reported, due to the strong environmental influence that affects defense production (Ballhorn et al., 2011; Gutbrodt et al., 2012). Phylogenetic distance quantifies the divergence time between a pair of species, and is a proxy for ecological differences (Cadotte et al., 2013). To calculate the phylogenetic distances, we constructed a phylogenetic tree for all the crops in the databases, from which we estimated the pairwise patristic distances between each pair of species (Supp. mat. N2, Fig. S1, Tables S7). When polycultures had more than two species, the phylogenetic and functional distances were estimated as the average distance between each pair of species.

2.2. Effect size

The effect size applied was the standardized mean difference between groups $((m1i\text{-}m2i)/spi)$, where, for the ith experiment, $m1i$ and $m2i$ were the means for a focal crop species growing in a polyculture and a monoculture, respectively, and spi the pooled standard deviation of these treatments (Hedges, 1981). In the analyses assessing herbivory pressure, a negative value for effect size indicated that polycultures reduced herbivore abundance or herbivory damage; in contrast, for the natural enemy analyses, a positive value for effect size indicated that polycultures favored predator and parasitoid abundance, or herbivore parasitism. We considered as non-independent the multiple measurements corresponding to the same types of response variable (i.e., herbivore abundance, herbivory damage, predator abundance, parasitoid abundance and herbivore parasitism) that were measured in the same plot or individual (e.g., percentage internode insect damage and number of herbivore exit holes), and measures repeated in time. In these cases, we combined all the outcomes using a fixed-effect model to obtain a mean composite effect size (Mengersen et al., 2012).

Additionally, as several studies reported both herbivore abundance and their natural enemies' abundance, we compared their ratio between mono- and polycultures. In this case, the effect size applied was the log transformed ratio of means $(\log(m1i/m2i))$, where $m1i$ and $m2i$ were the mean for herbivore abundance and natural enemy (predator or parasitoid) abundance, respectively, (Hedges et al., 1999). All effect sizes were estimated using the *escalc* function from the *metafor* R package (Viechtbauer, 2010) of the R software (v.4.2.0).

2.3. Data analysis

We analyzed the herbivory pressure and herbivore natural enemy databases separately, using the same main effects for both databases. We constructed a first type of model that evaluated the effect of increasing plant richness (i.e., polycultures *vs* monocultures) on the effect sizes of the different types of herbivory pressure and natural enemy response. We included response type as a moderator variable, the categories being herbivore abundance and herbivory damage for the herbivory pressure model, and predator abundance, parasitoid abundance and herbivore

parasitism for the natural enemy model. We used the Q test of residual heterogeneity given by the model to evaluate whether variation among observations was real, and could be explained by some co-variables at observation level (e.g., functional and phylogenetic distances) (Borenstein et al., 2009). In the second type of model, we evaluated whether the functional distance between intercropped species influenced the effect sizes reported for herbivory pressure or herbivore natural enemies; pairwise functional distances between crops were estimated using the Jaccard dissimilarity index, for direct or indirect defensive traits, depending on the database. Finally, in the third type of model we evaluated the influence of phylogenetic distance between intercropped species on herbivory pressure or natural enemy response. As the functional and phylogenetic distances are continuous variables, in the second and third model types we used a meta-regression approach (Borenstein et al., 2009). We could not evaluate the interactions between functional distance–response type and phylogenetic distance–response type because the variability within some of the subgroups was very low. The only interaction we could test was between functional distance and response type for the herbivory pressure effect sizes.

For the subset of studies that reported herbivore abundance and predator or parasitoid abundance, we evaluated whether the strength of the ratio herbivore abundance: natural enemy abundance differed between mono- and polycultures. In this case, the effect size was the logarithm of the ratio, and the type of crop system was entered in the model as the only moderator. Additionally, we evaluated the effect of the following factors that could bias the results: the presence of *Zea mays* ("maize or corn") in the polycultures (due to the high number of studies including this species), the region where the primary studies were carried out (temperate *vs* tropical), and the length of the life cycle of the crops in the polycultures (annual *vs* perennial). In the last case, we classified a polyculture as perennial when at least one species was perennial. In models that analyzed the influence of the presence of *Z. mays* or the region of cultivation, we also evaluated interaction with the functional distance between crops. However, we were not able to test the interaction between the presence of *Z. mays* or the region and the phylogenetic distances or the interaction between the life cycle and the functional and phylogenetic distances because of the lack of variability within subgroups.

Because we calculated more than one effect size for each study and for each polyculture species composition, in all cases we applied meta-analytic/regression multivariate random models (Konstantopoulos, 2011); in this way the observations, studies, and species composition of the polyculture nested within the study were considered random effects. We used the method of restricted maximum likelihood (REML), and the *rma.mv* function from the *metafor* package (Viechtbauer, 2010) of the R software (v.4.2.0); codes are shown in Supplementary material (R codes).

We also evaluated whether functional distances changed proportionally with phylogenetic distances by applying a Mantel test for dissimilarity matrices and the Pearson method (Goslee, 2010). The Mantel tests were carried out between the functional and phylogenetic distance matrices that contained the 55 plant species included in our study. We evaluated the correlation between the phylogenetic distance matrix and the matrices of functional distance calculated for direct defensive traits, indirect defensive traits, and direct and indirect defensive traits. The analyses were run using the *mantel* function from the *vegan* package (Oksanen et al., 2008) of the R software (v.4.2.0).

Lastly, we evaluated possible publication bias in both databases, as studies with non-significant results and/or small sample sizes (i.e., large error) have a low probability of being published (Borenstein et al., 2009). For this, we visually observed the relationship between effect sizes and standard errors using a funnel plot, and applied a rank correlation test for funnel plot asymmetry (Borenstein et al., 2009). In the absence of publication bias, points should be symmetrically distributed around the mean effect size (Jennions et al., 2012). In addition, we

applied the "trim and fill" method which adjusts the missing values, and estimates the overall effect size and the variance that might have been found in the absence of publication bias (Duval and Tweedie, 2000). We then compared the results obtained from this method with those obtained from a fixed model constructed to evaluate the global effect of polycultures on herbivory pressure and natural enemy response. We used the functions *funnel*, *ranktest* and *trimfill* from the *metafor* package (Viechtbauer, 2010) of the R software (v.4.2.0).

3. Results

In total, our herbivory pressure database included 107 records belonging to 36 studies, 52 commercial and non-commercial plant species and 53 polyculture species compositions (A1; Table S1), whereas the natural enemy database comprised 84 records corresponding to 18 studies, 32 commercial and non-commercial plant species and 31 polyculture species compositions (A1; Table S2), with some studies being included in both databases. Plant species belonged to phylogenetically dispersed angiosperm families (i.e., 14 families), most of them were annual herbs, but woody plants and perennial herbs were also represented. In all cases, herbivores and their natural enemies were arthropods. *Z. mays* was sown in polycultures in 60.3 % and 44 % of the records from the herbivory pressure and the herbivore natural enemy databases, respectively, regardless of whether it was the main crop or not. The herbivory pressure database incorporated studies from 18 countries (Fig. S2), from which 38 % belonged to temperate regions and 62 % to tropical regions, while the natural enemy database included studies from 10 countries (Fig. S2), with records being equally distributed among temperate and tropical regions. Only 28 % and 21.4 % of the records from the herbivory pressure and herbivore natural enemy databases, respectively, comprised polycultures with at least one perennial species. The studies included in both databases were performed under field conditions in experimental plots or farms, and the plot scale was very variable (e.g., $64 m^2$, $4000 m^2$, $100 m^2$; Tables S1 and S2). In most of the studies, crops were arranged in alternate rows, in additive or substitutive design, and no insecticides were applied (Tables S1 and S2). Finally, both mono- and polycultures were always exposed to similar conditions.

Herbivore abundance was, on average, lower in polycultures than in monocultures ($Z = -4.61$, $P < 0.0001$) (i.e., negative estimated average effect size (SMD)), and the moderator analysis indicated that polyculture arrays reduced herbivore abundance and herbivory damage similarly ($Q_{M1} = 0.01$, $P = 0.94$). The estimated average effect size ($\pm$ SE) was -0.89 ± 0.19; 95 % CI [-1.27, -0.51] for herbivore abundance, and, -0.91 ± 0.25; 95 % CI [-1.39, -0.43] for herbivory damage (Fig. 1a). The residual heterogeneity test showed high variability among effect sizes ($Q_{119} = 585.14$, $P < 0.0001$).

The level of herbivore parasitism was higher in polycultures than monocultures ($Z = 2.05$, $P = 0.04$), and no difference was observed regarding the effect of polyculture on herbivore parasitism, parasitoid abundance and predator abundance response ($Q_{M2} = 2.43$, $P = 0.30$). The estimated average effect sizes $\pm$ SEs and 95 % CIs for herbivore parasitism, parasitoid abundance and predator abundance were 0.55 ± 0.27, [0.02, 1.07]; 0.13 ± 0.27, [-0.40, 0.67]; and 0.09 ± 0.18, [-0.28, 0.45], respectively (Fig. 1b). The residual heterogeneity test suggested high variability among effect sizes ($Q_{81} = 300.58$, $P < 0.0001$).

Greater functional distances between intercropped species had a marginal negative effect on the overall herbivory pressure response variables ($Z = -1.90$, $P = 0.06$; -1.36 ± 0.72 [-2.77, 0.04]; Fig. 2a). Specifically, functional distance influenced negatively herbivore abundance ($Z = -2.21$, $P = 0.03$; -1.76 ± 0.80 [-3.33, -0.20]), but influenced positively herbivory damage ($Z = 2.04$, $P = 0.04$; 3.77 ± 1.85 [0.15, 7.40]; Fig. 3). In contrast, there was no evidence that functional distance influences natural enemy related responses ($Z = 1.38$, $P = 0.17$; 0.6797 ± 0.4906, [-0.2820, 1.6413]; Fig. 2b). Phylogenetic distance between intercropped species did not affect the level of herbivory
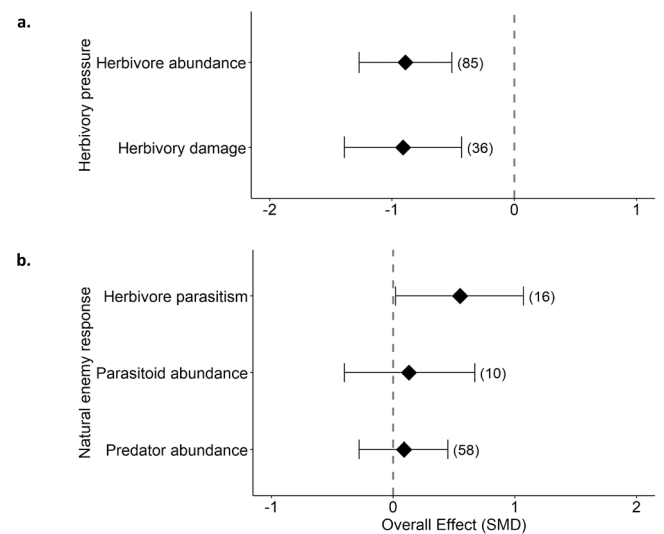

Fig. 1. a) Herbivory damage and herbivore abundance on focal plants were lower in polycultures than monocultures. b) Herbivore parasitism in polycultures was greater than in monocultures; however, predator abundance and parasitoid abundance were similar in poly- and monocultures. Diamonds represent the overall effect in standardized mean difference (SMD), and bars show the 95 % confidence intervals estimated by multivariate random models. The number in brackets is the sample size for each model.

pressure ($Z = 0.57$, $P = 0.57$; 0.0004 ± 0.0007, [-0.0009, 0.0017]; Fig. 4a) or natural enemy response ($Z = 0.92$; $P = 0.36$; 0.0006 ± 0.0006, [-0.0006, $- 0.0018$]; Fig. 4b).

The ratio herbivore abundance: natural enemy abundance was, on average, positive for both mono- and polycultures (2.22 ± 0.90, [0.46, 3.98]; 1.85 ± 0.88, [0.12, 3.58], estimate average effect size $\pm$ SE and 95 % CI, for mono- and polycultures, respectively), and its strength did not differ between the two types of crop systems ($Q_{M1} = 0.93$, $P = 0.34$). Regarding the evaluation of possible biases, we observed no influence of *Z. mays* or the region of the primary study on the effect of polyculture on herbivore pressure or enemy response (Supp. mat. N3). Likewise, we observed no statistically significant interactions between the factors *Z. mays* or region and functional distance for herbivory pressure or natural enemy response models (Supp. mat. N3). However, the life cycle of plant species influenced the magnitude of the polyculture effect on herbivory pressure. Polycultures with both annual and perennial species suffered less herbivory pressure than monocultures. However, polycultures with perennial species were the most efficient in reducing herbivory pressure (Supp. mat. N3). The plant life cycle did not influence the effect of polyculture on natural enemy response, and did not interact with functional distance (Supp. mat. N3).

The matrices of functional and phylogenetic distances were correlated for direct defensive traits (*Mantel statistic r* $= 0.17$, $P < 0.001$), indirect defensive traits (*Mantel statistic r* $= 0.23$, $P < 0.001$), and direct and indirect defensive traits together (*Mantel statistic r* $= 0.27$, $P < 0.001$).

The funnel plots and asymmetry test showed a slight asymmetry in the two databases. Nevertheless, the tendency shown by the "trim and fill" method was similar to the effect of polyculture on herbivory pressure and natural enemy response with the fixed-effect model results. In the case of herbivory pressure, the estimated average effect size was significant and negative, but non-significant for natural enemy related models (Supp. mat. N4).

4. Discussion and conclusions

Increased plant diversity in agroecosystems has been demonstrated to enhance crop resistance to herbivore attacks through both bottom-up
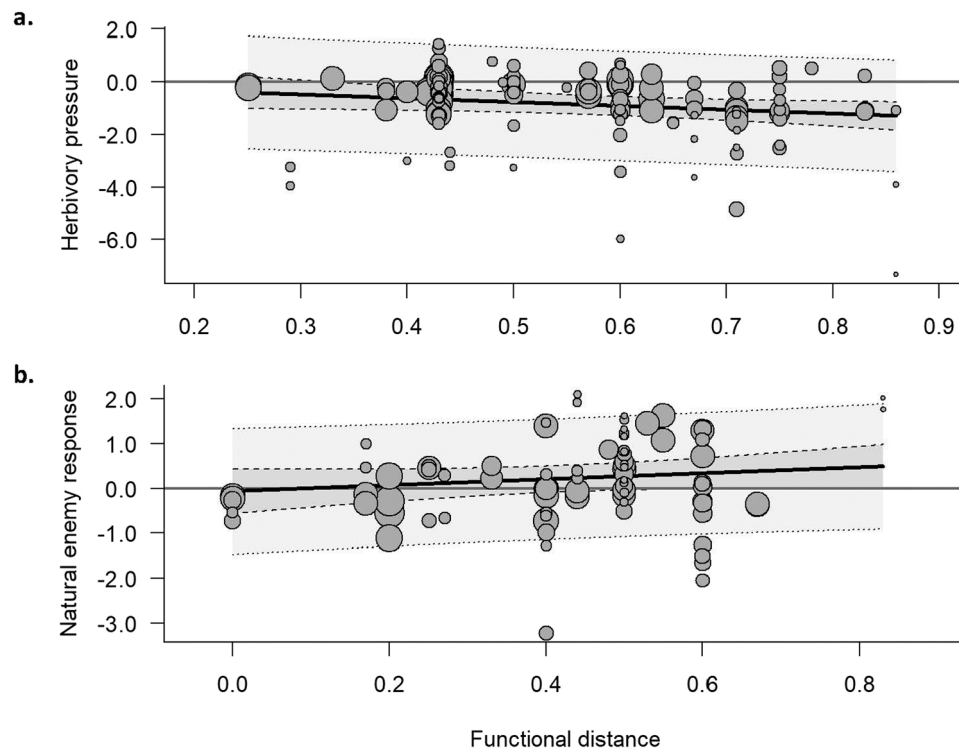
Fig. 2. a) The level of herbivory pressure on focal plants marginally decreased with increments in functional distance between intercropped species. b) The response of herbivore natural enemies to polycultures was not influenced by functional distance between plant species. Circles represent the effect size (i.e., standardized mean difference) of individual observations, and circle size the weight of each observation in the models. Light gray bands are the prediction interval bounds and dark gray bands are the 95 % confidence interval bounds.
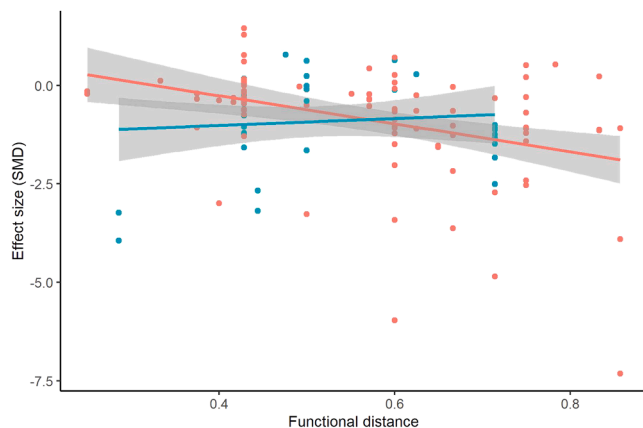

Fig. 3. The functional distance between intercropped species negatively influenced herbivore abundance (red points and trend line), but positively influenced herbivory damage (blue points and trend line). Gray bands are the 95 % confidence interval bounds.

and top-down mechanisms (Letourneau et al., 2011; Poveda et al., 2008). Using published data, here we applied meta-analytical approaches to assess the effect of crop diversity on both herbivory pressure and natural enemy response. Because plant species richness is frequently not enough to predict ecological functionality and promote pest suppression (Finney and Kaye, 2017; Flynn et al., 2011; Pearse and Hipp, 2009; Yguel et al., 2011), we assessed the role of functional and phylogenetic dissimilarity between intercropped species in crop resistance.

Our results added new evidence that polycultures contribute to reduced herbivory (Gurr et al., 2017; Letourneau et al., 2011; Tamburini et al., 2020). Focal plants growing in polycultures suffered less herbivory damage and hosted lower herbivore abundance than in monocultures. One possible explanation is top-down control exerted by herbivore natural enemies (Tooker and Frank, 2012), which is supported by our observation of higher levels of parasitized herbivores in polycultures than monocultures. However, we did not find evidence that predator or parasitoid abundance differs between polycultures and monocultures. Thus, higher herbivore parasitism in polycultures does not seem to be explained by higher parasitoid abundance. However, we cannot establish direct causality between response variables because in most cases they were not measured in the same studies. In any case, herbivore parasitism results should be handled with care because the sample size was relatively small. In addition, we observed herbivore abundance was greater than their natural enemies' abundance in both, mono- and polycultures.

In line with our results, Iverson et al. (2014) found that diversifying crop designs had a negative effect on herbivore abundance and plant damage, but no effect on predator abundance. Although polycultures may represent an optimal environment for herbivore predators and parasitoids, colonization of these environments may be limited by their proximity to sources of biodiversity, such as natural or semi-natural areas (González et al., 2020; Thies et al., 2003). Alternatively, many crop species are not grown in their biogeographic area of origin, and the native herbivore predators and parasitoids may not be adapted to respond to the attraction cues or exploit the floral resources offered by introduced crops (Chen, 2016). Although the top-down mechanism may be limited by all these factors, the bottom-up mechanisms driven by the crop functional traits may contribute to the reduction in herbivory pressure in polycultures (Tooker and Frank, 2012).

Functional diversity is linked to ecosystem services with multiple benefits to human beings (Díaz and Cabido, 2001). Here, we hypothesized that the more dissimilar the functional defensive traits of species in polycultures are, the greater the opportunities to deter herbivores and benefit herbivore natural enemies. Our results showed a marginal
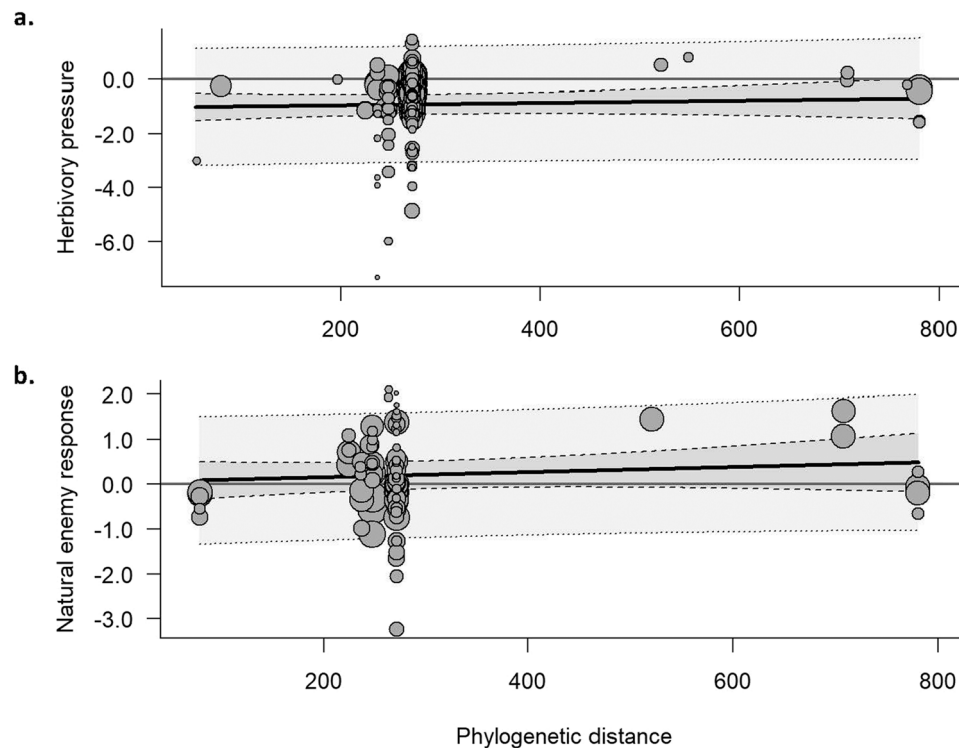
Fig. 4. The phylogenetic distance between intercropped species did not influence either the levels of herbivory pressure on focal crops (a) or the natural enemy response (b) in polycultures. Circles represent the effect size (i.e., standardized mean difference) of individual observations, and circle size the weight of each observation in models. Light gray bands are the prediction interval bounds and dark gray bands are the 95 % confidence interval bounds.

negative correlation between plant functional distance (i.e., defensive dissimilarity) and herbivory pressure. However, when we evaluated the different herbivory pressure responses separately, the influence of functional distance became more marked, and surprisingly, the two response variables showed opposite tendencies. At low values of functional distance, focal plants growing in polycultures suffered much less damage than in monocultures (negative effect size), but herbivore abundance was slightly greater in polycultures than in monocultures (positive effect size). As functional distance increased, the difference in herbivory damage between mono- and polycultures decreased, but never became positive. In contrast, at high values of functional distance, herbivore abundance in polycultures was much lower than in monocultures.

Herbivory damage and herbivore abundance tendencies may be explained by "resource dilution" and "resource concentration" effects, driven by herbivores specializing in focal crops. Herbivores with a narrow host range that are adapted to feeding on focal species are probably also capable of feeding on functionally similar (similar defensive mechanisms), but not on functionally dissimilar species (Mutz et al., 2022). Consequently, herbivory damage was "diluted" and uniformly distributed among species when they were functionally similar (both palatable), but was concentrated in only palatable species when intercropped species were dissimilar (Mutz et al., 2022; Otway et al., 2005). In contrast, as predicted by the Hambäck et al. (2014) model, herbivore abundance was similar in mono- and polycultures when species were functionally similar and herbivores were able to exploit them equally. However, when plants were functionally dissimilar, it could have been difficult for herbivores to locate palatable species due to the decrease in their density (substitutive design) (Root, 1973), or because they were hidden among non-palatable species (substitutive and additive design) (Castagneyrol et al., 2013). Therefore, herbivore abundance was higher in monocultures than in polycultures, as predicted by the resource concentration hypothesis (Kim et al., 2015; Root, 1973), Fig. 3. Aligning with our findings, Barbosa et al. (2009) observed a lower

abundance of herbivores on focal plants when the neighbors were non-palatable compared to them. Regarding damage on focal plants, they observed a reduction when neighbors were non-palatable and herbivores were mammals, but found no significant effect when herbivores were insects. This result contrasts with our own findings, as our database only included insect herbivores. Thus, our results highlight the importance of considering different response variables when evaluating herbivory pressure, since they can directly affect management decision-making.

On the other hand, natural enemy response did not correlate with functional distance. Unfortunately, as we mentioned in the methodology, we could not evaluate the effect of functional distance on the three natural enemy response types separately. This result suggests that predators and parasitoids did not respond to the number of resource types offered by plants in polycultures. According to Finney and Kaye (2017), the relative abundance of the different types of functional trait is frequently a better predictor of ecosystem functionality than trait number. Nevertheless, we did not include trait abundance in functional distance estimation because of methodological limitations. This may explain why functional distance, as estimated in this study, did not predict natural enemy response.

The phylogenetic distance between species may influence their functional similarity, due to conservation of ancestral traits. Indeed, phylogenetically related plant species often host similar herbivore assemblages (Gómez et al., 2010), and when they grow close to each other, herbivory pressure increases (Weiblen et al., 2006; Yguel et al., 2011). Hence, we expected the phylogenetic distance between intercropped species to influence the herbivory pressure exerted on plants growing in polycultures. Contrary to our expectations and to previous studies (Barbosa et al., 2009; Coco et al., 2022; Hahn and Cammarano, 2023), we found no evidence that phylogenetic distance influenced the level of either herbivore pressure (herbivore abundance and herbivory damage) or natural enemy response (predator abundance, parasitoid abundance and herbivore parasitism). As expected, we did observe a positive

correlation between phylogenetic and functional distance matrices for direct, indirect and all defensive traits together. However, the correlation strength was relatively weak in all cases ($r < 0.30$). This could reflect trait convergence, and/or the fact that functional differentiation is not always proportional to divergence times (Losos, 2008). Domesticated species evolved under both artificial and natural selection forces exerted by growers and the management practices they applied (e.g., nutrient and water supply) (Milla et al., 2015). Even though domestication target traits may vary among crops, many species underwent similar changes in traits that may influence ecological interactions (Milla, 2023). Thus, species domestication could promote trait convergence, and consequently, functional dissimilarity and phylogenetic distance are weakly correlated.

In agroecosystems, crop diversity is often increased to enhance crop resistance; however, the underlying mechanisms are still not well understood. The use of functional distance complemented by phylogenetic distance has been already applied by ecologists studying herbivory to characterize native ecosystems, with very interesting conclusions about plant resistance (e.g., Pearse and Hipp, 2009; Yguel et al., 2011); these factors are also being increasingly applied in research on productive systems (e.g., Coco et al., 2022; Hanh and Cammarano, 2023). In our study, we assessed the power of functional and phylogenetic distance to predict the resistance level of polycultures. Our results reaffirm that polycultures constitute a good strategy for reducing herbivory. Top-down control, via higher herbivore parasitism in polycultures than monocultures, may at least partly explain herbivory reduction. However, bottom-up mechanisms led by plant functional traits may also play a role. Functional dissimilarity of direct defensive traits between intercropped species influenced the polyculture effect on herbivory damage and herbivore abundance, but in opposite ways. However, functional dissimilarity in indirect defensive traits did not influence the response of natural enemies to polycultures. In turn, phylogenetic distance influenced neither herbivory pressure nor natural enemy response to polycultures.

Our results regarding functional distance provides valuable information for the design of sustainable agroecosystems that can minimize yield losses. Although intercropping functionally dissimilar species decreased the abundance of herbivores in polycultures, it did not directly impact on biomass loss. The best strategy to lessen productivity loss seems to be intercropping functionally similar species. Based on this recommendation, one difficulty farmers could face is knowing which species are functionally similar or dissimilar to each other. For this reason, it is essential that ecologists and botanists collect data on plant functional traits in free and open access databases (e.g., TRY). Collaboration between farmers and scientists is essential for polyculture design and the subsequent evaluation of its effectiveness.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data is available in supplementary material.

Appendix A. : Complete list of the references included in herbivory pressure and natural enemy response databases

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Appendix B. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108800.

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