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Spider guilds in a maize polyculture respond differently to plant diversification, landscape composition and stage of the agricultural cycle

Running title: Spider guild diversity in a polyculture landscape

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Abstract

1. Agroecosystem simplification for greater food production has led to the loss of ecosystem services such as pest control by natural predators. Agroecological practices such as plant diversification have shown excellent potential to improve the abundance and richness of crop predators such as spiders.

2. However, in agroecosystems with frequent disturbances such as annual crops, it is unknown whether the positive effect of plant diversification on spiders depends on the surrounding landscape and/or the stages of the agricultural cycle (*i.e.* periods with differences in vegetation, weather, and agricultural practices).

3. Here, we evaluated the effect and interaction of local management (plant diversification), landscape (forest areas), and agricultural cycle on the richness and abundance from the main spider guilds of a maize polyculture in Mexico.

4. We found that greater crop diversification (*i.e.* addition of legumes and leafy plants) caused a greater abundance of *ground-hunting* spiders. We also show that a larger area of forest around the crop favors a greater richness and abundance of *ground* and *vegetation hunting* spiders.

5. We found that each stage of the agricultural cycle had a different spider richness and abundance, *ground hunters* were more common at the beginning of the cycle (*e.g.* winter) while *vegetation hunters* and *web-builders* were more common during the peak developmental stages of the crops (*e.g.* fructification).

6. Our findings support the idea that to foster functionally diverse spider communities that potentially enhances natural pest control, we must jointly manage plant elements within the

crop, in the surrounding landscape, and considering the high dynamics of spider communities throughout the agricultural cycle.

Key words: guilds, local management, forest, dispersal, temporal variation.

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Introduction

The use of conventional practices to boost food production has contributed to the decline of biodiversity in agricultural fields (Altieri & Trujillo, 1987; Lichtenberg et al., 2017). This decline in agrodiversity has resulted in the loss of ecosystem services, such as natural pest control through the activity of indigenous predators (Altieri & Trujillo, 1987; Gallé et al., 2019). This issue holds significant importance as it is estimated that global crop productivity could decrease by up to 40% due to damages inflicted by pest insects (FAO, 2021). Polycultures based on traditional systems such as "*milpas*" (*i.e.* polyculture involving maize, beans, and squash as primary crops; Zizumbo et al., 2012) can be a viable alternative for enhancing the biodiversity within agricultural fields (Altieri & Trujillo, 1987; Isakson, 2009), since these systems maintain a relatively high plant diversity by cultivating and promoting a mixture of species while minimizing input usage, particularly pesticides, which can be harmful to predators (Birkhofer et al., 2013). However, predators such as spiders exhibit complex responses to factors that shape their diversity in agricultural crops (Birkhofer et al., 2013). Therefore, to create effective management strategies that promote taxonomically and functionally predator diverse communities for natural pest control, a better understanding of the dynamics determining spider communities in polycultures is necessary.

Agroecological management has been proposed as an alternative for sustainable agriculture, aiming to maintain crop biodiversity (Wezel et al., 2014; Martínez-Camacho et al., 2022). Crop diversification, achieved by incorporating plant species that enhance plant heterogeneity and prey availability (Sunderland & Samu, 2000), is an agroecological practice employed to foster increased spider richness and abundance (Samu, 2003;

Geldenhuys et al., 2021). However, it is likely that the effect of plant diversification on spider richness and abundance is dependent on the composition of the landscape surrounding the crops (*i.e.* natural and semi-natural habitat areas; Batáry et al., 2011; Galloway et al., 2021). For instance, Galloway et al., (2021) showed that spider richness only responded positively to agroecological management in perennial crops surrounded by simplified landscapes (*i.e.* little forest cover). Within these simplified landscapes, an increased availability of shelters and prey, promoted by a higher diversity of local plants, is more important than in crops surrounded by diverse regional organisms sources (Batáry et al., 2011). The success of implementing practices to enhance predator abundance and contribute to pest control, may depend on the context of the landscape where the cultivation plots are established (Batáry et al., 2011).

In annual crops, significant temporal variation occurs due to the intra-annual dynamics of agricultural practices (*e.g.* plowing), weather conditions, and vegetation (Kennedy & Storer, 2000). This intra-annual variability in crops, combined with species phenology, creates a temporal dynamic in spider communities, leading to increased species abundance and richness during the peak developmental stages of the crops (Triquet et al., 2022). In addition, this temporal variation in the crops creates frequent disturbances that cause spiders to become highly dependent on local and regional shelters (Birkhofer et al., 2013; Gavish-Regev et al., 2008). A more pronounced positive effect of agroecological practices on spider diversity is expected during stages characterized by greater disturbance to communities, such as winter, coinciding with the majority of crop harvesting and extreme weather (Gavish-Regev et al., 2008; Sunderland & Samu, 2000). Most studies consider that the effect of local and regional management on spiders in agricultural crops is static (Birkhofer et al., 2013; Lichtenberg et al., 2017). However, the effectiveness of management practices appears contingent on the specific stages of the agricultural cycle in which they are implemented (Schmidt et al., 2005; Schmidt & Tscharntke, 2005). This would partly explain why some studies have not detected clear positive effects of augmenting local vegetation and landscape heterogeneity on spider diversity (Sunderland & Samu, 2000).

Spiders use different hunting and dispersal strategies (Cardoso et al., 2011), and thus the response to factors that determine the spider communities in agricultural crops differs between guilds (Michalko & Pekár, 2016; Michalko & Košulič, 2019). Notably, some groups of spiders with high dispersal capacity (*e.g. web-building spiders* such as Lyniphiidae, up to ≈ 30km; Thomas et al., 2003) can rapidly recolonize crops after a disturbance associated with an agricultural practice or the weather (Dauber et al., 2005; Feber et al., 2015; Picchi et al., 2016). Conversely, guilds with more limited dispersal abilities, which disperse only a few meters or kilometers by walking (*e.g. ground hunters* such as Lycosidae, Decae, 1987), are expected to be more dependent on high local plant diversity and the landscape. For example, Feber et al., (2015) showed that the richness and abundance of *ground-hunting* spiders (Lycosidae) responded positively to local organic management (suspended use of agrochemicals) and the number of natural habitats in the landscape compared to other guilds with high dispersal capacity. This indicates that, it is necessary to understand how the abundance and diversity of each spider guild are differentially affected by factors associated with the local mangement, landscape, and agricultural cycle to promote abundant and functionally diverse communities in the case of annual crops.

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In the present study, we evaluated in a field experiment the effect of diversification of a traditional Mexican maize polyculture (*milpa*) on the richness and abundance of the main spider guilds (*ground hunters*, *vegetation hunters,* and *web-builders*). Specifically, we analyzed how such effect of plant diversification is modulated by the forest areas surrounding the crops and the stages of the agricultural cycle. Given the intra-annual variation of the maize polyculture, we expected the spider communities to have higher species abundance and richness during the peak developmental stages of the crops (Triquet et al., 2022). We also postulated to find higher spider richness and abundance in crops with higher plant diversification and larger surrounding forest areas during stages with extreme weather and scarcity of prey and shelters (stages of initial development and crop senescence) (Sunderland & Samu, 2000). Finally, given that the response of spiders depends on their hunting and dispersal strategies (Feber et al., 2015), we expected the positive effect of crop diversification and perennial vegetation areas in the landscape (forests) on spider richness and abundance to be stronger in guilds with low-mid recolonization capacity (*ground* and *vegetation hunters* Feber et al., 2015).

Methods

Study area and plots

We conducted the study in a maize polyculture area located in the community of Ocotepec, Ayahualulco, Veracruz, Mexico (19°21'38.24" N, 97° 9'41.78" W; 2280 m.a.s.l.) (Figure 1). The landscape of the study area is mostly dominated by large maize-growing areas (in a polyculture with beans and squash called *milpa*), pastures/shrubs (areas with grasses and shrub species, mostly *Baccharis conferta* Kunth), a few remnants of natural forest, and some pine-growing areas (Figure 1). The milpas planted in the study area are exclusively used to feed the farmers and their families, their management is conventional (with the use of industrial fertilizers and plowing), and corn grain yields reach approximately 2,300 kg·ha^{-1} (Martínez-Camacho et al., 2022). The agricultural cycle in the area occurs from March to November and the corn is harvested only once a year.

For this study, we selected the plots of an agroecological diversification experiment established by our research team since 2018. These are 12 plots of 200 m^2 each (20 m x 10 m) with three levels of interspecific plant diversification (4 replicates/plots per level). The plot selection was done in collaboration with producers that volunteered in the project *Mano Vuelta*, whose objective was to improve the sustainability of the production of food for the rural families of the region (Martínez-Camacho et al., 2022). The participants were informed of the required characteristics and the objectives of the project, and voluntarily offered land where the experimental plots could be set up for several consecutive years. The diversification experiment was established in the 12 plots at least 4 years prior to the present study and was associated with an agroecological management. This agroecological management was carried out by the owners of the plots, who were weekly joined by the *Mano Vuelta* project team, and consists of completely organic fertilization with a fermented fertilizer (*bokashi*) prepared *in situ* with stover, sheep manure, ash, pulque (locally fermented agave beverage as a source of microorganisms), soil, and unrefined brown sugar, as well as the complete absence of tillage practices. The three levels of plant diversification were: level 1 (M-B-S) = plots planted with the basic crop triad of maize (*Zea mays* L.), fat bean (*Phaseolus dumosus* Macfady), and squash (*Cucurbita ficifolia* Bouché); level 2 (M-B-S + L) = plots planted with the basic triad and additional legumes (black beans

[*Phaseolus vulgaris* L.], peas [*Pisum sativum* L.], and faba beans [*Vicia faba* L.]); and level 3 (M-B-S + L + H) = plots planted with the basic triad, legumes, and additional leafy plants (chard [*Beta vulgaris* L. var. cicla] and coriander [*Coriandrum sativum* L.]) (Martínez-Camacho et al., 2022). The legumes and leafy plants used for the diversification of the plots were selected because they are crops frequently observed in local backyard vegetable gardens and some milpas, and to add nutrient diversity to the diet of local families. The plot diversification was carried out at specific moments of the agricultural cycle: legumes were added during winter and leafy plants were added during the developmental stage (*see below*). Data from the 2021 agricultural cycle were used for this study.

Milpa **agricultural cycle**

For this study, the 12 plots were sampled during 5 stages of the 2020-2021 *milpa* agricultural cycle (Figure 1). Each stage represents an important period of the phenology of the crops. **Winter** (December-January): corresponds to the moment after the collection of maize, beans, and squash. Winter legumes are planted in the plots with diversification levels 2 and 3 (faba beans and peas); **Planting** (February-March): the basic crop triad is planted in all plots. Winter legumes are maturing during this season; **Growth** (April-August): winter legumes are harvested, and leafy plants are planted in the plots with diversification level 3. The plants of the basic triad germinate, grow, and flower; **Fructification** (September-October): the plants of the triad are mature and bear fruits, and the leafy plants are harvested in the plots with diversification level 3; **Harvest** (November): maize, beans, and squash are harvested and completely removed from all plots (Figure 2).

The samplings were preferably conducted towards the middle of each stage of the agricultural cycle.

Spider community sampling and taxonomic identification

Spider sampling was performed with three capture methods commonly used to catch these predators (Ubick et al., 2005, Benamú & Viera, 2023), which were used to sample the two main strata of the cultivation plots: the ground (pitfall traps) and the vegetation layer between 0.10 m and 1.80 m (manual capture and foliage beating). The combination of these techniques provides an adequate sampling completeness of the different spider guilds that occur in natural ecosystems and cultivation crops (Sørensen et al., 2002; Jiménez-Valverde & Lobo, 2005; Picchi, 2020). During each stage of the cycle, we established five sampling points in each plot arranged in the shape of a cross: one near each corner of the plot and one in the center. The sampling points were separated from the edge of the plot by at least two meters and from each other by at least five meters. Unbaited pitfall traps were placed in each point, which were left active during 48 hours with a lethal dose of water with salt and detergent. One day after setting up the pitfall traps, we conducted the manual collection and foliage beating in each plot with the help of the farmers. We performed the manual collection for an approximate searching time of 10 minutes around each sampling point. Foliage beating was performed with a circular net, 50 cm in diameter, and a wooden stick to beat the vegetation around each sampling point for an approximate time of 5 minutes. All specimens were collected with pooters and tweezers and preserved in jars with 95% ethanol.

Adult and subadult spiders were classified into morphospecies according to their morphological characteristics (somatic and sexual). We only taxonomically identified subadult (with developed somatic characteristics) and adult individuals, and pooled their values. When possible, individuals were assigned to a species using taxonomic keys (Ubick et al., 2005; World Spider Catalog, 2021). The individuals that could not be assigned to a species were identified as morphospecies at the lower taxonomic level possible. The morphospecies codes are exclusive to this study. For the analyses, we used a previously proposed classification of spider trophic guilds (Cardoso et al., 2011; Feber et al., 2015), where species and morphospecies were grouped into three large groups: *ground hunters*, *vegetation hunters*, and *web-builders*. These spider guilds differ in dispersal capacity, agroecosystem stratum, and hunting strategy, which would potentially result in a differential response to the management, landscape, and agricultural cycle of the milpa (Feber et al., 2015; Méndez-Castro et al., 2020; Quijano-Cuervo et al., 2022). G*round hunters*, dominated by spiders of the family Lycosidae, are species mainly associated with the ground that disperse by walking and are active hunters. V*egetation hunters*, dominated by species of the families Salticidae and Thomisidae, have an intermediate dispersal capacity, mainly occupy the vegetation stratum associated with crop and herbaceous plants, and are also active hunters. As members of the *Pachygnatha* genus have forfeited their capacity to hunt through webs in their adult stage, they have been classified as *Vegetation hunters* for this study. In other studies, it is assumed that these spiders hunt on the ground (Harwood *et al.*, 2005; Svobodová *et al.*, 2013); however, in this study, we did not capture or observe individuals of this species on the ground. *Web-builders*, dominated by the family Lyniphidae, have a high dispersal capacity by *ballooning*, are mainly associated with the vegetation stratum of the milpa (except spiders of the genus *Erigone* assigned to *ground hunters*), and hunt using their webs (Carvalho & Cardoso, 2014; Wu et al., 2017; Méndez-Castro et al., 2020; Quijano-Cuervo et al., 2022).

Characterization of the landscape surrounding the *milpas*

To characterize the landscape surrounding the study plots, we created a land-use cover map using a supervised classification of the Sentinel satellite image (downloaded from earthexplorer.usgs.gov, and composed of spectral bands 2, 3, 4, 8; with 10-meter resolution) of the area surrounding the study plots (*e.g.* Nivedita Priyadarshini et al., 2018). We generated a map of the four main land-use covers in the area: *crops* (milpas), *forest* (remnants and cultivated), *pastures/shrubs*, and *urban zones* (houses and roads) (Figure 1). For the classification, we first carried out a manual training that consisted in generating training polygons of each land-use (based on previous knowledge of the area) to subsequently obtain the spectral signatures of the pixels. The spectral signatures of each land-use were used to make a classification of the composite satellite image with the method of maximum likelihood, assigning equal probability to all classes and a rejection fraction of 5%. All analyses were performed in QGIS 3.26 (QGIS Development Team, 2023). To select the buffer extent where the effect of landscape composition on spider community was stronger (scale of effect, *sensu* Jackson & Fahrig, 2015), we constructed generalized linear models ("*poisson*" error and "*log*" link function). For these models, we used as dependent variables the richness and abundance of the whole spider community (*i.e.* without discriminating by guild) and as explanatory variable the extent of the surface of each land-use in 8 buffers of different diameter. The buffers around the plots ranged from a 50-meter radius from the center of the plot to 400 meters, increasing every 50 meters. We defined a maximum buffer extent of 400 meters, since larger buffer extents almost completely overlapped between plots. We constructed a model for each buffer diameter (8 buffers) of each land-use (four land-uses) for a total of 32 models for each dependent variable (richness and abundance). We used the R^2 (coefficient of determination) of the models as the criterium to select the scale of effect (*i.e.* the spatial extents that best explain the patterns encountered, Jackson & Fahrig, 2015), which in the case of our study was 300 meters. We found that the best fit occurred in this extent (300 meters, *see* table S2), which agrees with the intermediate extents found to be significant in previous studies with spiders in winter wheat fields (95 m – 3000 m, Schmidt et al., 2008). In order to ensure that the proximity of the study plots did not contain spatial autocorrelation that caused problems of lack of spatial independence in the linear models (see below) (Zuckerberg et al., 2020), we evaluated the autocorrelation of the model residuals using classical variography following Negrete-Yankelevich & Fox, (2015). We fitted theoretical variograms (*spherical*, *exponential* and *gaussian*) using weighted least squares to determine if there were aggregation patches in the model residuals using the package *geoR* (Ribeiro & Diggle, 2018) in R (R Core Team, 2020).

Models of the relationship between spider richness and abundance and local management, landscape, and agricultural cycle

We evaluated the effect of plot diversification, landscape, and agricultural cycle on spider abundance (*negative-binomial* error) and richness (*poisson* and *negative-binomial* error) using generalized linear models (GLMs) with the *glm* function of the R package *stats*

(R Core Team, 2022). Given the high correlation between the extents of landscape habitats (*Pearson's* $r_{\text{(forest - crops)}} = -0.95$, $p = <0.001$; *Pearson's* $r_{\text{(forest - urban zones)}} = -0.90$, $p = <0.001$, *Pearson's* $r_{\text{(forest - pastures)}} = -0.11$, $p = 0.39$), and the recognized importance of the forest as a reservoir of spider diversity (Schmidt et al., 2005), we only used as landscape variable the forest extent surrounding the plots. Our full model included the following explanatory variables: agricultural cycle stage as a factor with five levels, plant diversification treatment as a factor with three levels (three diversification treatments), forest extent as continuous variables measured in the 300-m buffer, and all the second order interactions of these variables. Given that the values of *forest* extent differed by several orders of magnitude compared to the response variables, we rescaled that variable for our models by dividing each value by the root mean square using the *scale* function in R. To obtain the *minimum adequate model*, we used the *dredge* function of the R package *MuMIn* to generate an automated model selection (Bartoń, 2022). This function selects the models with greater explanatory power and lower number of parameters among all independent variable combinations and their interactions (to the second order in our case). In the case of our study, we selected as plausible models those with the lowest AIC value and that differed in at least two units from the null model (variable= variable's mean) (Burnham & Anderson, 2002). During the initial phases of analysis, we built mixed models with temporal replicates as a random factor, however the variation associated with this factor did not have a significant contribution and therefore was not retained in the final models (*see* Table 1, Figure S1). We verified that the final models satisfied the assumptions of normality, homoscedasticity, and absence of overdispersion (in the case of *poisson* distribution) and spatial autocorrelation of residuals. These analyses were performed for the whole spider community and for each of the three spider guilds (*ground hunters*, *vegetation hunters*, and *web-builders*).

Results

Spider fauna in the *milpas*

We collected a total of 1933 spiders grouped into 68 morphospecies (50% identified to genus) and 13 families (*see* supplementary Table S1). Lycosidae was the most abundant family in the study milpas (1221 individuals, 63%), while Linyphiidae had the highest number of morphospecies (14 species, 20%). Two morphospecies of the family Lycosidae (*Pardosa* sp1 and sp2) and one of Lyniphiidae (*Erigone* sp1) had the highest number of individuals in the entire study, contributing with 64% of total abundance (Table S1). *Ground-hunting* spiders were dominated by one species of the genus *Pardosa* (*P*. sp1, 53%), while *vegetation hunters* were dominated by one species of the family Anyphaenidae (*Anyphaena* sp2, 43%), and *web-builders* were dominated by a species of the family Theridiidae (*Theridion* sp3, 3%) (Table A.2).

Effect of plant diversification, landscape, and agricultural cycle on the richness and abundance of spider guilds

We found that plant diversification, forest vegetation areas in the surrounding landscape, and agricultural cycle had an additive, but not interactive, effect on the richness and abundance of the spider guilds or the total spider community (Table 1, Figures 3 and 4). The plots diversified with legumes and leafy plants always had a higher abundance of the entire spider community and *ground hunters* compared to the other plant diversification treatments (Table 1, Figure 3). Spider abundance was positively associated with the forest area surrounding the crop plots, in the entire community ($\beta_{slope} = 0.69$) and in the *ground hunter* ($\beta_{slope} = 1.11$) (Table 1, Figures 3 and 4). The richness of the entire community ($\beta_{slope} = 0.13$) and of *vegetation hunters* ($\beta_{slope} = 0.18$) was also positively associated with the forest area surrounding the crop plots (Figure 4A and 4C). Richness and abundance of *web-builder* spiders were not affected by plant plot diversification or forest areas around *milpas*.

With respect to temporal variation, the richness of the entire spider community and the richness and abundance of *vegetation hunters* and *web-builders* increased during the intermediate stages of the agricultural cycle, that is, during the growth and fructification stages (Table 1, Figure 4C-F). In contrast, *ground-hunting* spiders showed higher abundance during the winter and planting stages (Table 1, Figure 4B).

Discussion

It has been proposed that crop diversification promotes the presence of spiders (Sunderland & Samu, 2000), which provide ecosystem services such as pest control (Michalko et al., 2019). However, the effect of these agroecological practices likely depends on the composition of the landscape surrounding the crops (Galloway et al., 2021) and the stage of the agricultural cycle in annual crops (Birkhofer et al., 2013; Schmidt et al., 2005; Sunderland & Samu, 2000). In the present study, we found no evidence of such dependence, as each factor operating at the plot (*plant diversification*) and landscape scale (*forest areas*), as well as the agricultural cycle, have an additive and independent effect on spider richness and abundance. Furthermore, as predicted, the effect of these factors differs

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between spider guilds with different hunting and dispersal strategies (*e.g.* Feber et al., 2015).

4.1 Effect of crop diversification and surrounding landscape on spider guilds

Our results partially agreed with our hypothesis, since we found that plant diversification in the maize polyculture only had a positive effect on the total abundance of the spider community and the abundance of the dominant spider guild of *ground hunters*, but not on the species richness of these groups. In addition, contrary to our prediction, this positive effect of diversification did not depend on the extent of the surrounding forest or pasture areas or the stage of the agricultural cycle. Spiders are a group that is sensitive to local vegetation heterogeneity (Tews et al., 2004), and crop diversification benefits the presence of these predators by increasing the number of suitable sites in terms of climate, prey, and shelter from predators (*review by* Sunderland & Samu, 2000). Other studies have also shown that the diversification of maize crops with legume and other plant species promotes an increase in local spider abundance (Coll & Bottrell, 1995; Gliessman, 2014; Midega et al., 2008), and this increased abundance may have direct implications on the density-dependent control of maize pests (Letourneau, 1986, 1987, 1990). It is likely that we did not detect a significant interaction between local management and the surrounding landscape because, in this annual system, in addition to medium-sized forest or pasture areas (*300 m around*), spiders could also depend on more local shelters. Live fences or herbaceous fields at the edge of or within cultivation plots might constitute refuges from where spiders can rapidly colonize the crops (Denys & Tscharntke, 2002; Amaral et al., 2016), particularly dominant spiders such as Lycosids (Schmidt-Entling & Döbeli, 2009).

We found that the abundance of *ground-hunting* spiders was positively affected by crop diversification with two plant groups: legumes (*P. vulgaris*, *P. sativum*, *V. faba*) and leafy plants (*B. vulgaris*, *C. sativum*). This suggests that, in order to have a positive effect, it is necessary to generate a minimum level of vegetation structure or crop diversification at least at two relevant stages of the agricultural cycle (Sunderland & Samu, 2000; Poveda et al., 2008). The addition of a dense vegetation structure close to the ground promoted by leafy plants may have benefited *ground-hunting* spiders in particular, and not the other spider guilds with more specific vegetation structure requirements (Rypstra et al., 1999; Benamú et al., 2017). Moreover, it is possible that the addition of legumes in winter, a stage when ground spiders are more likely to occur (Nyffeler & Benz, 1988), promotes the accumulation of these spiders in the diversified plots from the first stages of the agricultural cycle and they remain there throughout the cycle.

Similarly to our result, other studies have shown that only spider abundance responds positively to local crop management (Sunderland & Samu, 2000; Rusch et al., 2014; Dassou & Tixier, 2016), and that species richness is not always benefited by plot management through diversification (Beaumelle et al., 2021). The two plant groups used for crop diversification may not have provided enough variety in vegetation structure and prey (Poveda et al., 2008) for different spider species to occur in the plots. The purpose of the crop diversification in the present study was not only to promote the presence of predators, but also to improve the chemical properties of the soil and make an integral contribution to the diet of the farmers (Martínez-Camacho et al., 2022). It has been proposed that, to promote an increase in spider richness, it is necessary to identify and provide the functionally important elements of plant diversity that benefit different guilds (*e.g.* different strata such as herbs and shade trees), rather than promoting plant diversity *per se* (Landis et al., 2005; Poveda et al., 2008). An increase in spider diversity, and not only in the abundance of dominant species, may likely result in a greater contribution to pest control in crops (Letourneau et al., 2009), since more spider species with different hunting strategies, preferred strata, and temporal dynamics would cover a large part of the spectrum used by pests in cultivation crops.

We found that a larger forest area in the surrounding landscape had a positive relationship with the richness and abundance of the entire spider community and the *vegetation* and *ground hunter* guilds. Different studies have demonstrated the positive effect that large extents of forest areas have on spider diversity, which may be due to natural habitats around cultivation plots serving as regional sources of spiders and providing additional prey during stages of low food availability and severe weather conditions, especially in annual crops (Birkhofer et al., 2013; Schmidt et al., 2008, 2005; Schmidt & Tscharntke, 2005). As predicted, the landscape had a stronger effect on *ground-hunting* spiders (*i.e.* relationship with a steeper slope, *see* Figures 3-4 and Table 1), which have a lower dispersal capacity than *vegetation hunters* and *web-builders* (Pearce et al., 2005; Feber et al., 2015). These results agree with previous evidence; for example, a study conducted in winter wheat fields where Feber et al., (2015) found that the positive effect of the landscape on spider abundance was stronger in terrestrial spiders with a limited dispersal capacity such as those of the family Lycosidae. It has been shown that spiders with low dispersal capacity colonize crops from their shelters in the landscape (Lemke & Poehling, 2002; Schmidt et al., 2005), which results in a higher probability of these spiders arriving to plots with a higher number of and greater proximity to forest areas.

4.2 Effect of the agricultural cycle on spider richness and abundance

There is little evidence related to the effect of the agricultural cycle of crops on spider communities (*but see* Benamú et al., 2017; Triquet et al., 2022). In the present study, we found that the possible variation in habitat availability, weather conditions, and agricultural practices (Kennedy & Storer, 2000) may be associated with the guild-dependent variation in spider abundance and richness among the stages of the agricultural cycle. The richness and abundance of *web-building* and *vegetation-hunting* spiders were higher during the intermediate stages of the agricultural cycle. Consistent with our results, Triquet et al., (2022) showed that spider diversity was higher towards the middle of the annual cycle of maize, which was when the crop plants were at their peak of vegetative development (*growth* and *fructification* stages). In our study scenario, during these intermediate periods of the agricultural cycle, in addition to crop plants being at their peak developmental time (*maize*, *beans,* and *squash*), other vegetation strata that increase the heterogeneity of the plots may be present, such as strata herbaceous plants (*personal observation*), which farmers remove by hand only at the beginning of crop growth to prevent competition, and are known to particularly benefit spider guilds that hunt in the vegetation (Benamú et al., 2017; Benamú & Viera, 2023).

In contrast to other guilds, *ground-hunting* spiders were more abundant during the initial stages of the agricultural cycle, that is, during winter and planting. It is known that spiders of the family Lycosidae are an important component of winter communities because they are generalists and multivoltine and, unlike other spider families, find shelter from the weather in elements such as mulch (Nyffeler & Benz, 1988). This finding is critical for pest management in annual crops, since the colonization and massive occurrence of spiders during the early stages of the agricultural cycle may help mitigate the damage caused by pests (Birkhofer et al., 2013; Gavish-Regev et al., 2008). With the objective of promoting the presence of diverse spider guilds during most stages of the agricultural cycle, and thus ensure a potential control of pest populations in all strata (*i.e.* vegetation and ground), cultivation plots should not have bare soil and should have a diverse vegetation cover, for instance, by adding mulch covers, planting winter crops (as in our study), or creating nearby shelters for spiders, such as live fences or herbaceous fields (Birkhofer et al., 2013; Triquet et al., 2022, Halaj et al., 2000; Rypstra et al., 1999).

5. Conclusions

Our findings empirically highlight that spiders are a predator group with a complex response to local factors and the surrounding landscape (Schmidt et al., 2008; Birkhofer et al., 2013), and that multiple vegetation elements and strata should be used, both at the plot (*e.g.* vegetation edges, herbaceous plants, added plants, crop density) and landscape (*e.g.* forest proximity and surface area or connectivity) scales in order to promote functionally diverse spider communities in agrolandscapes. It is also necessary consider the complex temporal dynamics related to variation in weather conditions, crop development, and agricultural practices (*e.g.* tillage and harvest). All these elements (vegetation added to plots, forest cover, and stages of the agricultural cycle) had an additive, but guild-dependent, effect on the spider community in our study.

We suggest that, in highly dynamic systems such as annual crops, plant diversification in cultivation plots should aim to generate diverse vegetation strata throughout the agricultural cycle, which would promote the presence of diverse spider communities (Sunderland & Samu, 2000). Many of the efforts to improve agrodiversity have been concentrated at a local scale (plot or *parcela* [piece of rural or agricultural land] management) (Sunderland & Samu, 2000; Wezel et al., 2014), without considering the effect of the surrounding landscape on the communities of beneficial organisms such as natural controllers (Gonthier et al., 2014). The findings of the present experimental study, together with previous evidence (Schmidt & Tscharntke, 2005; Gallé et al., 2019), indicate the need to consider the use of multiple elements of agricultural landscapes (Salman et al., 2019) in order to improve the presence of diverse spider guilds, since this may potentially reduce the use of pesticides (Wezel et al., 2014).

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Figures and tables

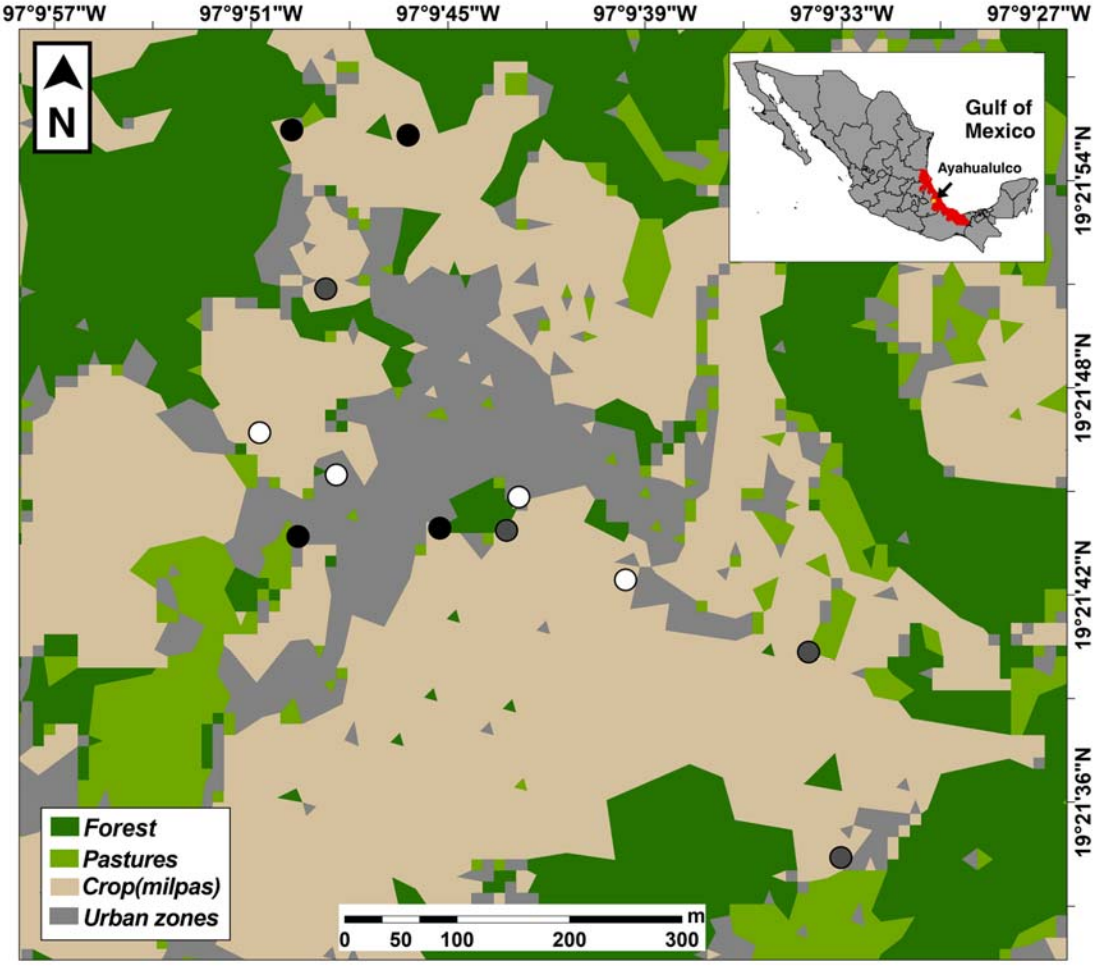

Figure 1. Study area location and map of the main land uses. Land uses were generated from the supervised classification of a Sentinel image (10-meter resolution). Colors: black= plots with the basic triad Maize-Bean-Squash (M-B-S), dark grey= plots with the basic triad and added legumes (M-B-S + L), white= plots with the basic triad and added legumes and leafy plants (M-B-S + L+H).

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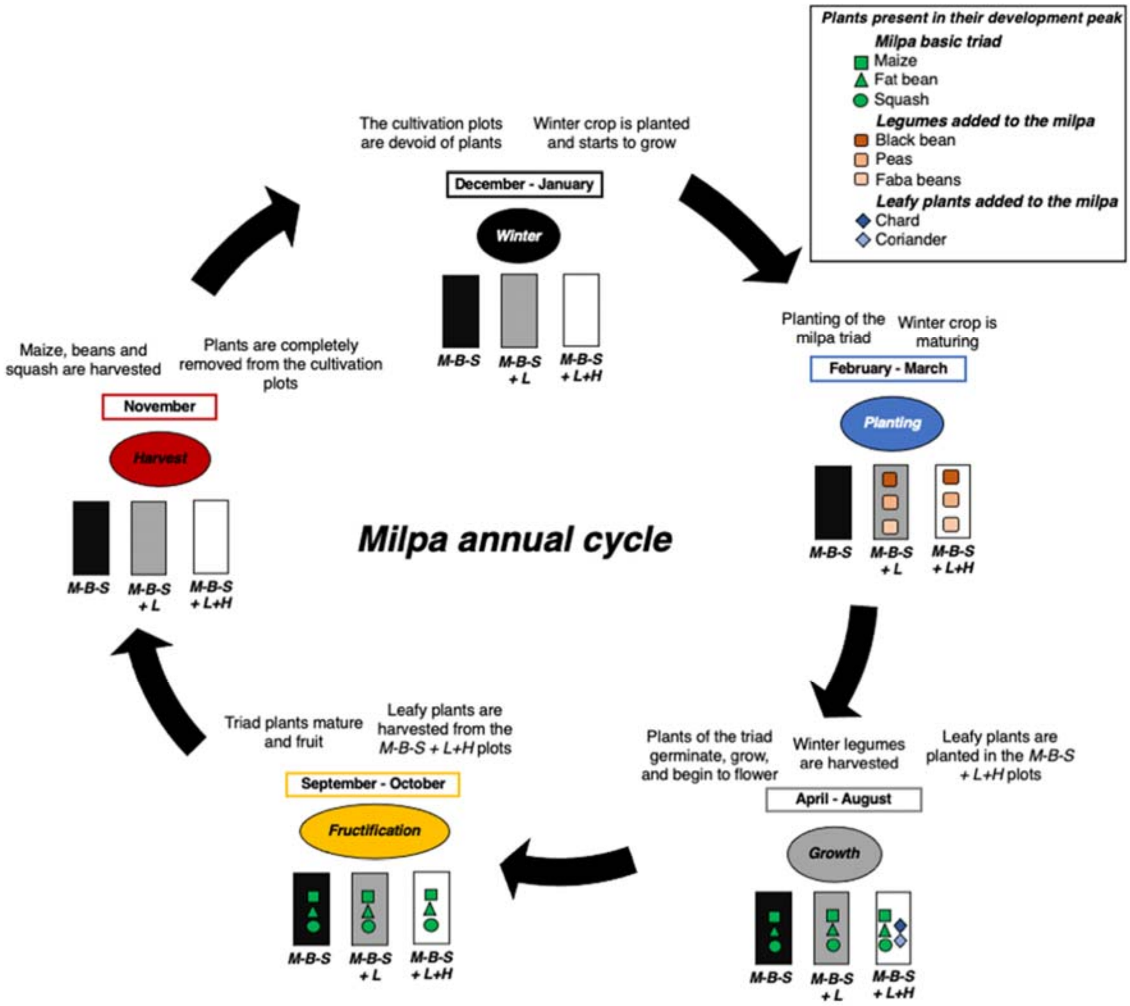

Figure 2. Summary of the stages of the *milpa* agricultural cycle. The stages were divided based on the most important events during the months of crop development. Note that the presence of some plant species in certain stages depends on the level of plant diversification. Abbreviations: M-B-S = plots with the basic triad Maize-Bean-Squash, M-B-S + L = plots with the basic triad and additional legumes, M-B-S + L+H = plots with the basic triad, legumes, and added leafy plants.

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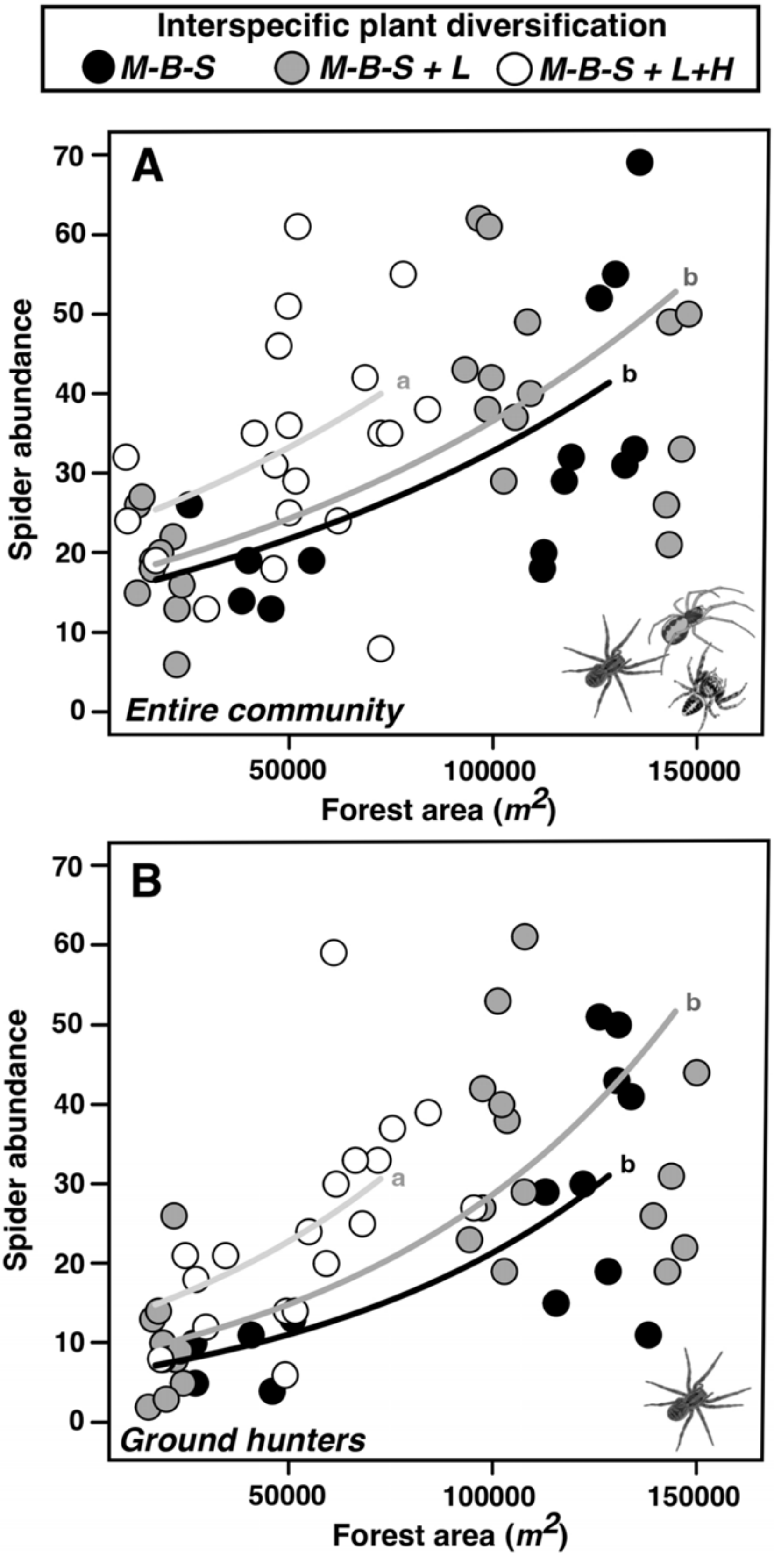

Figure 3. Effect of plant diversification and the surrounding landscape on the abundance of the entire spider community and *ground-hunting* spiders. M-B-S = plots with the basic triad Maize-Bean-Squash, M-B-S + L = plots with the basic triad and additional legumes, M-B-S + L+H = plots with the basic triad, legumes, and added leafy plants. Different letters to the right of the fitted lines indicate significant differences between the intercepts. Note that we plotted different trendlines with different intercepts but with the same slopes, which denotes lack of interaction between factors.

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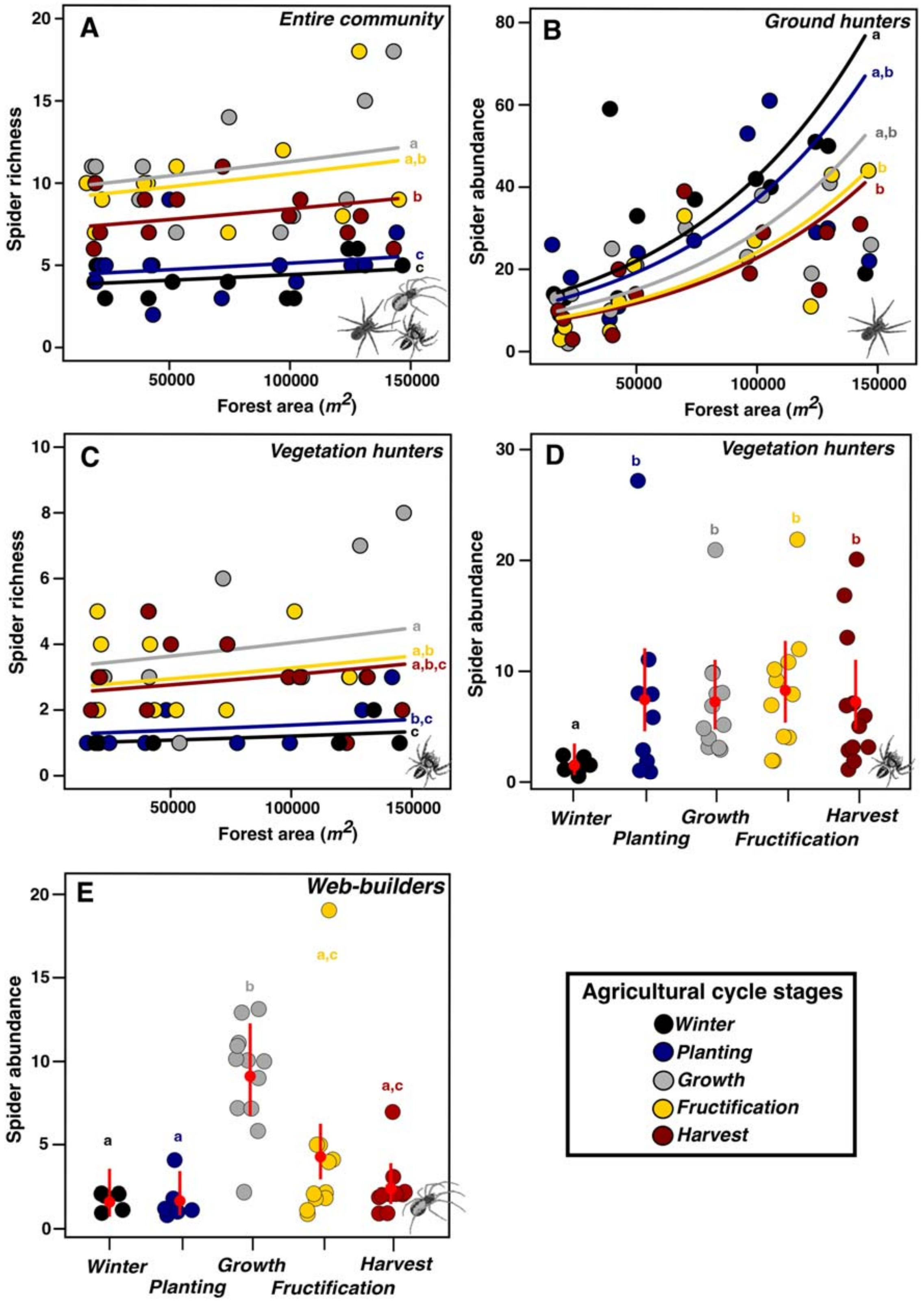

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Figure 4. Effect of the milpa agricultural cycle and the landscape on the richness and abundance of the entire spider community and the spider guilds. Different letters to the right of the fitted lines indicate significant differences between the intercepts. Note that we plotted different trendlines with different intercepts but with the same slopes, which denotes lack of interaction between factors. The error lines in figures D and E correspond to 95% confidence intervals. We only plotted the guilds with significant variation in the models.

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Table 1. Summary of the generalized linear models (GLMs) of the richness and abundance of the spider community and the spider guilds.

Spider guild	Dependent variable	Plant diversification (α - *intercepts*)	Landscape (β - *slopes*)	Agricultural cycle (α - *intercepts*)	AIC final model	AIC Null model (ΔAIC)	AIC Mixed model (ΔAIC)
Entire community	***Abundance*** ***(Ln [No. Ind. · plot^{-1}])***	M-B-S (2.66) M-B-S + L (2.77) M-B-S + L+H (3.36)	Forest (0.69)	ni	467.4	490.4 (22.9)	469.3 (1.9)
	Richness ***(Ln [No. Sp. · plot^{-1})***	ni	Forest (0.13)	Winter (1.32) Planting (1.47) Growth (2.26) Fructification (2.19) Harvest (1.97)	265.8	315.3 (49.4)	306 (40.1)
Ground hunters	***Abundance*** ***(Ln [No. Ind. · plot^{-1}])***	M-B-S (1.46) M-B-S + L (1.76) M-B-S + L+H (2.18)	Forest (1.11)	Winter (2.05) Planting (1.91) Growth (1.67) Fructification (1.48) Harvest (1.46)	442.2	479.3 (37)	441.5 (0.7)
Vegetation hunters	***Abundance*** ***(Ln [No. Ind. · plot^{-1}])***	ni	Forest (0.32)	Winter (0.95) Planting (1.94) Growth (1.87) Fructification (1.71) Harvest (1.40)	314.7	320.3 (5.5)	335.4 (20.6)
	Richness ***(Ln [No. Sp. · plot^{-1}])***	ni	Forest (0.24)	Winter (0.04) Planting (0.42) Growth (1.17) Fructification (0.65) Harvest (0.51)	181.8	193.6 (11.7)	205.6 (23.7)
Web-builders		ni	ni	Winter (0.76)	256.7	278.7 (21.9)	281.1 (24.3)

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Abundance (*Ln [No. Ind. · plot^{-1}]*)			Planting (0.61) Growth (2.31) Fructification (2.09) Harvest (1.83)			
Richness (*Ln [No. Sp. · plot^{-1}]*)	ni	ni	Winter (0.45) Planting (0.45) Growth (1.45) Fructification (1.51) Harvest (1.21)	190.2	204.1 (13.8)	217.5 (27.2)

Abbreviations: ni, factor not included in the model. Indicates that the variable has little explanatory power according to AIC; ΔAIC= AIC_{null} - the $\text{AIC}_{\text{final}}$ (AIC_{null} is the AIC of the response variable explained by its mean), M-B-S = Basic milpa triad [maize, beans and squash], M-B-S + L = Basic milpa triad and added legumes [black beans, peas, and faba beans], M-B-S + L+H = Basic milpa triad, added legumes, and leafy plants [chard and coriander]. Note that the intercept values are expressed as logarithms.

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Supplementary material

Table S1. Total abundance of spiders in the plant diversification treatments and the agricultural cycle stages.

Guilds	**Families**	**Species**	**Interspecific plant diversification**			**Agricultural cycle stages**					
			M-B-S	*M-B-S + L*	*M-B-S + L+H*	*Winter*	*Planting*	*Growth*	*Fructification*	*Harvest*	*Total*
Ground hunters	Lycosidae	*Arctosa* sp1	34	35	53	75	2	3	28	14	122
	Lycosidae	*Arctosa* sp2	2	0	0	1	0	0	1	0	2
	Corinnidae	Corinnidae sp1	0	1	0	0	0	1	0	0	1
	Linyphidae	*Erigone* sp1	27	85	40	33	34	31	34	20	152
	Linyphidae	*Erigone* sp2	1	0	0	0	1	0	0	0	1
	Gnaphosidae	Gnaphosidae sp1	1	1	0	0	0	0	1	1	2
	Gnaphosidae	Gnaphosidae sp2	0	0	1	0	0	0	1	0	1
	Gnaphosidae	*Haplodrassus* sp1	1	0	0	0	1	0	0	0	1
	Lycosidae	Lycosidae sp1	0	1	0	0	1	0	0	0	1
	Lycosidae	Lycosidae sp2	0	1	0	0	0	0	1	0	1
	Lycosidae	*Pardosa* sp1	192	308	245	266	186	106	86	101	745
	Lycosidae	*Pardosa* sp2	100	137	113	1	93	117	58	81	350
	Corinnidae	*Scotinella* sp	0	0	1	0	0	1	0	0	1
	Trachelidae	*Trachelas* sp1	3	3	4	0	0	3	3	4	10
Vegetation hunters	Anyphaenidae	*Anyphaena* sp1	2	2	0	1	1	2	0	0	4
	Anyphaenidae	*Anyphaena* sp2	37	33	30	0	0	28	39	33	100
	Anyphaenidae	*Anyphaena* sp3	7	0	2	0	0	9	0	0	9
	Thomisidae	*Misumenoides* sp1	1	5	4	0	0	8	1	1	10
	Thomisidae	*Misumenoides* sp2	4	3	2	0	0	4	4	1	9
	Miturgidae	Miturgidae sp1	1	0	0	0	1	0	0	0	1
	Salticidae	*Paraphidippus aurantius*	5	9	5	0	0	16	3	0	19
	Salticidae	*Phidippus audax*	1	1	1	0	0	3	0	0	3
	Salticidae	Salticidae sp1	0	3	1	1	1	1	1	0	4
	Salticidae	Salticidae sp2	0	15	46	0	60	0	0	1	61
	Salticidae	Salticidae sp3	0	2	0	0	0	1	1	0	2
	Salticidae	Salticidae sp6	1	1		0	0	0	0	2	2
	Tetragnathidae	*Pachygnatha* sp1	14	31	29	7	3	5	25	34	74
	Tetragnathidae	*Pachygnatha* sp2	5	5	6	0	0	6	2	8	16

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	Tetragnathidae	*Pachygnatha* sp3	1	1	1	0	0	1	1	1	3
	Tetragnathidae	*Pachygnatha* sp4	3	0	0	0	0	0	3	0	3
	Tetragnathidae	*Pachygnatha* sp5	8	8	0	0	0	0	11	5	16
	Thomisidae	*Xysticus* sp1	0	1	1	0	0	2	0	0	2
	Thomisidae	*Xysticus* sp2	1	0	0	0	1	0	0	0	1
	Thomisidae	*Xysticus* sp3	0	0	1	0	0	1	0	0	1
	Thomisidae	*Xysticus* sp4	0	0	1	0	0	0	0	1	1
Web builders	Araneidae	Araneidae sp1	0	1	0	0	0	1	0	0	1
	Araneidae	Araneidae sp2	0	2	1	0	0	3	0	0	3
	Araneidae	Araneidae sp3	1	0	0	0	0	1	0	0	1
	Araneidae	Araneidae sp4	1	0	0	0	0	0	1	0	1
	Araneidae	Araneidae sp5	3	0	0	0	0	0	3	0	3
	Araneidae	*Araneus* sp	0	1	0	0	0	0	1	0	1
	Araneidae	*Eriphora orizabensis*	1	1	1	0	0	0	0	3	3
	Theridiidae	*Latrodectus* sp	0	1	0	0	0	1	0	0	1
	Linyphidae	Linyphiidae sp1	3	7	4	3	1	5	3	2	14
	Linyphidae	Linyphiidae sp2	1	5	3	5	0	1	2	1	9
	Linyphidae	Linyphiidae sp3	0	1	2	0	1	0	0	2	3
	Linyphidae	Linyphiidae sp4	1	0	1	0	2	0	0	0	2
	Linyphidae	Linyphiidae sp5	0	2	0	0	1	0	1	0	2
	Linyphidae	Linyphiinae sp6	7	1	2	1	0	0	4	5	10
	Linyphidae	Linyphiidae sp7	0	2	0	0	0	1	1	0	2
	Linyphidae	Linyphiidae sp8	1	0	0	0	0	1	0	0	1
	Linyphidae	Linyphiidae sp9	1	0	0	0	0	0	1	0	1
	Linyphidae	Linyphiidae sp10	2	0	0	0	0	0	2	0	2
	Linyphidae	Linyphiidae sp11	0	0	1	0	0	0	1	0	1
	Linyphidae	Linyphiidae sp12	0	0	1	0	0	0	1	0	1
	Pholcidae	Pholcidae sp	0	1	0	0	0	0	0	1	1
	Tetragnathidae	*Tetragnatha* sp1	0	0	3	0	0	0	1	2	3
	Tetragnathidae	Tetragnathidae sp1	0	1	4	0	5	0	0	0	5
	Tetragnathidae	Tetragnathidae sp2	1	0	0	0	0	1	0	0	1
	Tetragnathidae	Tetragnathidae sp3	0	1	0	0	0	1	0	0	1
	Theridiidae	Theridiidae sp1	1	2	0	0	0	3	0	0	3
	Theridiidae	Theridiidae sp2	7	0	2	0	0	6	3	0	9
	Theridiidae	Theridiidae sp3	4	4	4	0	0	3	4	5	12
	Theridiidae	Theridiidae sp4	2	0	0	0	0	0	2	0	2
	Theridiidae	*Theridion* sp1	3	5	4	1	0	4	3	4	12

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Theridiidae	*Theridion* sp2	5	16	8	0	0	28	1	0	29
Theridiidae	*Theridion* sp3	17	16	28	0	0	49	12	0	61
Theridiidae	*Theridion* sp4	0	0	1	0	0	0	0	1	1

Table S2. Model results (GLM) used to determine the scale of effect.

Variable	Scale	R^2 Abundance	R^2 Richness
Crop area	*50 m*	0.018	**0.029**
	100 m	0.026	0.025
	150 m	0.002	0.027
	200 m	0.038	0.012
	250 m	0.088	0.007
	300 m	**0.129**	0.006
	350 m	0.128	0.002
	400 m	0.017	0.001
Forest area	*50 m*	0.033	0.004
	100 m	0.087	0.001
	150 m	0.142	0.001
	200 m	0.133	0.012
	250 m	0.154	0.033
	300 m	**0.171**	**0.037**
	350 m	0.133	0.011
	400 m	0.080	0.003
Pasture area	*50 m*	0.002	0.004
	100 m	0.000	**0.005**
	150 m	0.001	**0.005**
	200 m	0.014	**0.005**
	250 m	0.054	0.004
	300 m	**0.081**	0.003
	350 m	0.031	0.001
	400 m	0.022	0.000
Urban area	*50 m*	0.090	0.007
	100 m	0.142	0.006
	150 m	**0.180**	**0.015**
	200 m	0.108	0.004
	250 m	0.092	0.001
	300 m	0.087	0.001
	350 m	0.059	0.001
	400 m	0.104	0.001

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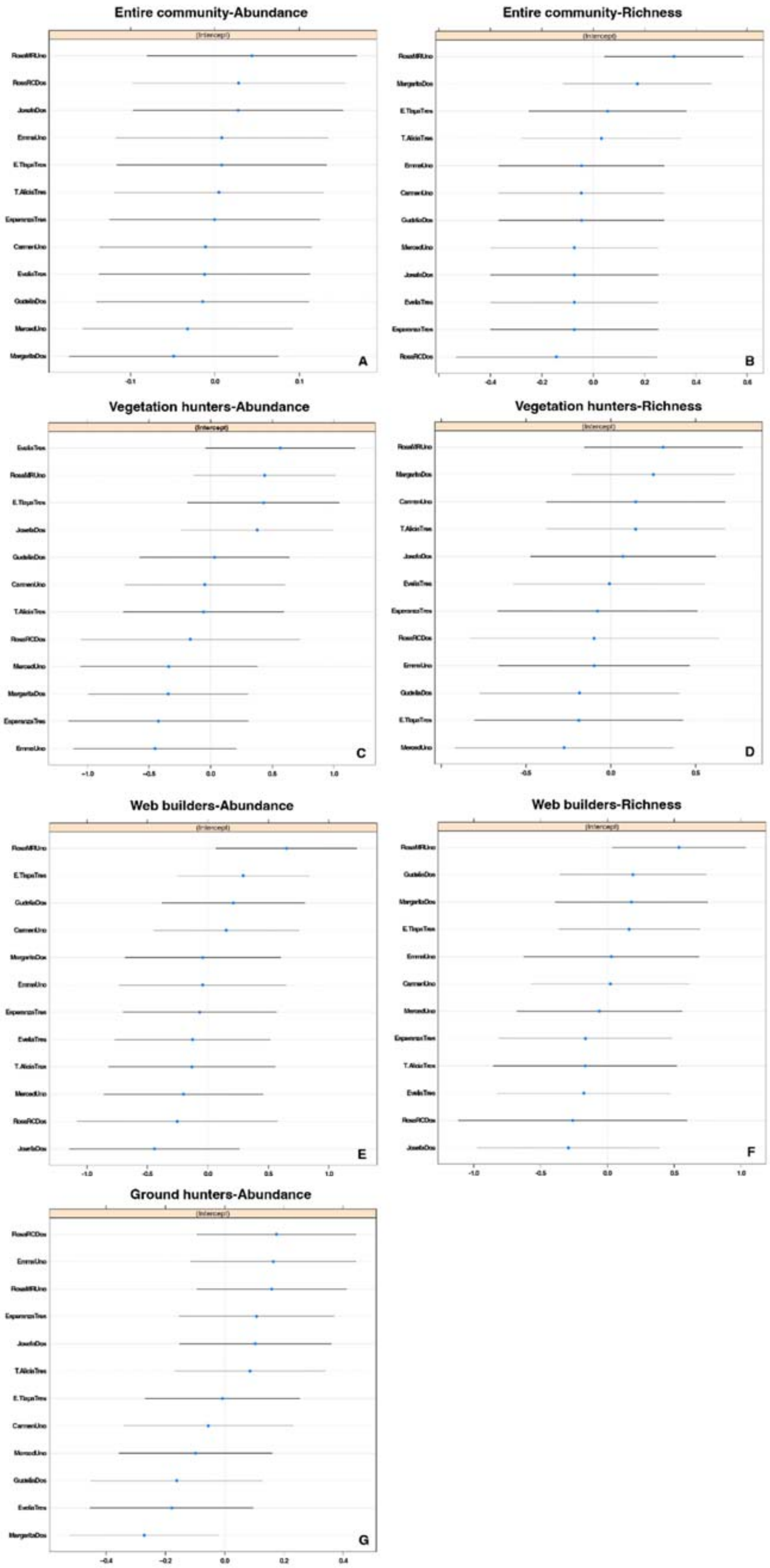

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Figure S1. Variation associated with plots included as a random factor in the mixed models built in the initial analysis phases.

Table S3. Pairwise comparison of the averages estimated in the linear models for the richness and abundance of the different spider guilds.

Guilds	**Variable**	**Pairwise comparation**	**|Mean difference|**	***p* value**	***p* value corrected**
Entire community	Abundance	D0 - D1	1.67	0.4	
		D0 - D2	7.61	**0.006***	**0.016***
		D1 - D2	5.93	**0.01***	**0.03***
	Richness	Winter - Planting	0.59	0.44	
		Winter - Growth	5.85	**0.00000001***	**0.005***
		Winter - Fructification	5.23	**0.0000002***	**0.01***
		Winter - Harvest	3.4	**0.0002***	**0.025***
		Planting - Growth	5.26	**0.0000004***	**0.015***
		Planting - Fructification	4.64	**0.000007***	**0.02***
		Planting - Harvest	2.81	**0.002***	**0.03***
		Growth- Fructification	0.61	0.6	
		Growth - Harvest	2.44	**0.029***	**0.03***
		Fructification - Harvest	1.82	0.1	
Ground hunters	Abundance	D0 - D1	1.48	5.94E-02	
		D0 - D2	4.59	0.0001*	0.01*
		D1 - D2	3.10	0.005*	0.03*
		Winter - Planting	0.98	0.45	
		Winter - Growth	2.45	**0.04***	0.02
		Winter - Fructification	3.36	**0.004***	0.01*
		Winter - Harvest	3.44	**0.002***	0.005*
		Planting - Growth	1.46	0.19	
		Planting - Fructification	2.37	**0.028***	0.02
		Planting - Harvest	2.45	**0.019***	0.015
		Growth- Fructification	0.91	0.33	
		Growth - Harvest	0.99	0.27	
		Fructification - Harvest	0.07	0.92	
Vegetation hunters	Abundance	Winter - Planting	5.94	**0.001***	**0.02***
		Winter - Growth	5.74	**0.001***	**0.015***
		Winter - Fructification	6.77	**0.0007***	**0.005***
		Winter - Harvest	5.74	**0.001***	**0.01***
		Planting - Growth	0.19	0.93	
		Planting - Fructification	0.82	0.74	
		Planting - Harvest	0.19	0.93	
		Growth- Fructification	1.02	0.66	
		Growth - Harvest	0.00	1	
		Fructification - Harvest	1.02	0.66	

	Richness	Winter - Planting	0.26	0.6	
		Winter - Growth	2.36	**0.004***	**0.01***
		Winter - Fructification	1.67	**0.02***	**0.015***
		Winter - Harvest	1.51	**0.02***	**0.025**
		Planting - Growth	2.09	**0.002***	**0.005***
		Planting - Fructification	1.40	**0.025***	0.02
		Planting - Harvest	1.24	0.039	0.03
		Growth- Fructification	0.68	0.31	
		Growth - Harvest	0.8	0.19	
		Fructification - Harvest	0.16	0.79	
Web builders	Abundance	Winter - Planting	0.06	0.93	
		Winter - Growth	7.48	**0.0001***	**0.015***
		Winter - Fructification	2.67	**0.0302***	**0.03***
		Winter - Harvest	0.80	0.38	
		Planting - Growth	7.41	**0.00007***	**0.010***
		Planting - Fructification	2.6	**0.024***	**0.025***
		Planting - Harvest	0.73	0.39	
		Growth- Fructification	4.81	**0.003***	**0.020***
		Growth - Harvest	6.68	**0.00002***	**0.005***
		Fructification - Harvest	1.87	0.064	
	Richness	Winter - Planting	0.13	0.84	
		Winter - Growth	2.55	**0.012***	0.01
		Winter - Fructification	1.89	**0.03***	0.02
		Winter - Harvest	0.70	0.33	
		Planting - Growth	2.41	**0.01***	0.005
		Planting - Fructification	1.75	**0.03***	0.02
		Planting - Harvest	0.56	0.4	
		Growth- Fructification	0.65	0.4	
		Growth - Harvest	1.85	**0.017***	0.015
		Fructification - Harvest	1.19	0.09	