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Por medio de la presente se hace constar que el C.

LUIS GUILLERMO QUIJANO CUERVO

Presentó su examen para obtener el grado de **Doctor en Ciencias** el día 29 de agosto de 2023, defendiendo el trabajo titulado: **"Biodiversidad de arañas en cafetales y milpas agroecológicas: integrando la descripción de nuevas especies y el estudio de los patrones y procesos ecológicos"**, bajo la Co-Dirección de la Doctora Simoneta Negrete Yankelevich y el Doctor Wesley Francisco Dáttilo da Cruz. El examen fue aprobado satisfactoriamente y su documentación oficial se encuentra en firma para ser entregada.

El examen de grado fue precedido por los integrantes de su Jurado de tesis:

Dr. Roger Enrique Guevara Hernández	**Presidente**
Dra. Simoneta Negrete Yankelevich	**Secretaria**
Dra. Dulce Rodríguez Morales	**Vocal**

A quienes agradezco su valiosa disposición y calidad académica con que contribuyeron de manera muy importante a la formación académica del Doctor Quijano Cuervo.

Para los fines que al interesado convengan se extiende la presente constancia a partir de hoy, veintinueve de agosto del año dos mil veintitrés. Cabe mencionar que este documento no es evidencia de haber cumplido con todos los requisitos administrativos para llevar a cabo la entrega de los documentos de grado.

Xalapa Enríquez, Veracruz a 29 de agosto de 2023.

Dr. Oscar Luis Briones Villarreal
Secretario de Posgrado

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Luis Guillermo Quijano Cuervo <luisquijanocuervo@gmail.com>

Agricultural and Forest Entomology - Decision on Manuscript ID AFE(2023)4734

1 mensaje

Allan Watt <onbehalfof@manuscriptcentral.com> 9 de noviembre de 2023, 11:43
Responder a: adw@ceh.ac.uk
Para: luisquijanocuervo@gmail.com
Cc: luisquijanocuervo@gmail.com, ekdelval@cieco.unam.mx, rogelio.macias@inecol.mx, wesley.dattilo@inecol.mx, simoneta.negrete@inecol.mx

Re: AFE(2023)4734 entitled "Spider guilds in a maize polyculture respond differently to plant diversification, landscape composition and stage of the agricultural cycle" by Quijano Cuervo, Luis; del Val, Ek; Macias Ordoñez, Rogelio; Dáttilo, Wesley; Negrete Yankelevich, Simoneta

Dear Dr. Quijano Cuervo,

Manuscript ID AFE(2023)4734 entitled "Spider guilds in a maize polyculture respond differently to plant diversification, landscape composition and stage of the agricultural cycle" which you submitted to Agricultural and Forest Entomology, has been reviewed.

The comments of the reviewers are included at the bottom of this letter. If the reviewer uploaded a file you can find it in your author centre at https://mc.manuscriptcentral.com/afe.

The reviewers have recommended revisions to your manuscript. Therefore, I invite you to respond to the reviewers' comments and revise your manuscript.

We also encourage authors to provide the title and abstract in an alternative language or languages to increase the accessibility of their work should it be published. Authors who wish to take advantage of this option should provide the alternative language title(s) and abstract(s) in the main document below the English language version of each.

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Once again, thank you for submitting your manuscript to Agricultural and Forest Entomology and I look forward to receiving your revision.

Sincerely,

Allan Watt
Editor, Agricultural and Forest Entomology
Bush Estate
Edinburgh
United Kingdom of Great Britain and Northern Ireland
EH26 0QB

Agricultural and Forest Entomology is a journal of the Royal Entomological Society. For more information about our portfolio of journals, please visit http://www.royensoc.co.uk/publications/index.htm

Associate Editor's Comments to Author:

Thank you for submitting your manuscript to Agricultural and Forest Entomology. All reviewers recognised the value of this work and believe that it could make a valuable contribution to the literature, but several key issues with the current presentation were raised.

I particularly agree with the reviewers who raise the presentation of the results as an area in need of improvement and additional clarity. Some more information is necessary regarding variability and the outcomes of the statistical tests used. The presentation of the results needs some justification and tweaking. I think the presentation of Table 1 needs some consideration too; where categorical variables are compared (e.g., diversification, agricultural cycle), these will be pairwise comparisons and thus the model should be releveled to account for each combination. The separation of taxa into web-builders, ground-hunters and vegetation-hunters needs some reconsideration or justification in line with Reviewer 2's comments. Resolving the placement of more ambiguous groups (i.e., Linyphiidae) requires some justification, ideally based on the taxa present at these sites.

Reviewer(s)' Comments to Author:
Reviewer: 1

Referees Comments
This manuscript investigates the impact of plant diversity in an annual crop system, agricultural cycle stage, and local forest cover on spider abundance and richness.

Overall, the manuscript is well written, and provides evidence to suggest land management for the improvement of biodiversity and ecosystem services, such as natural pest control, requires consideration of the landscape area. The sample collection is well explained and justified, though I would be intrigued to know at what point during each stage sampling took place - was this in the beginning, middle, or end of each stage? (This may have implications for the results). Figure 2 is a useful accompaniment for the planting cycle. However, more clarity is needed on what statistical methods were used to produce the values in the results. Specifically, it is not clear how alpha(intercept) and beta(slope) values were calculated from the glm methods used, with p values missing from the results section. It is also not very clear why the trend lines are plotted with the same slopes in figures 3 and 4 for each planting regime and cycle stage. In addition, the results for ground hunter richness are not included in the manuscript, or justified as to why this is missing. The discussion clearly places the study amongst existing literature and considers the wider applications. The topic is very current, and of interest to ecologists and entomologists. I think if these comments are addressed, this manuscript would be a great addition to the literature base.

Line 74: perhaps consider changing from "spider richness and abundance" to "spider richness". The cited paper by Galloway et al. (2021) states that while

heterogeneity of neighbouring vegetation did not greatly impact arthropod predators on organic farms, spider (and beetle) abundance was an exception to this (Discussion paragraph 4).
Line 328: change "(Figure 4C-D)" to "(Figure 4A and C)".
Line 343: related to first comment, the finding of an additive effect on spider abundance is corroborated by the cited literature (Galloway et al., 2021). The sentence starting on line 343 is phrased as though they have contradictory findings.

Reviewer: 2

Referees Comments
This paper explores spider communities in relation to the plant diversification of polycultures in Mexico and how these relationships potentially depend on the composition of surrounding landscape. The design involves three treatments and four replicates where data was collected during different phases of the cropping system. The design is good and the paper is generally well-written and easy to understand. However, I do have comments on the presentation of results and also some about the grouping of species.

First, a key aspect being investigated is the comparison between ground-hunters, vegetation-hunters and web-builders. Then, when reading the results, it is stated that the most abundant web-builders are Pachygnatha, but these don't build webs. Pachygnatha has lost the capacity to build webs and instead hunt on the ground. You also have a quite large group of unidentified Linyphiidae, where there is also some variability in the web-building. So, please adjust the groups.

My second major concern is about Table 1. Just presenting the slopes and intercepts is quite meaningless. You also need to include some measure of variability and some more statistical information. So, please add standard errors and other statistical information. Just having AICs is not particularly informative. This is important in order to evaluate which difference between treatments in Fig. 3 and 4 that are actually relevant.

Next, in Figs 3 and 4, the y-axis shows log-values of abundances. I strongly suggest that you include the actual values rather than log-values on the axis. You can still have it on a log-scale but values should be real. So, assuming base10, you have '1' instead of log(1)='0', '10' instead of log(10)='2' and so on. This procedure helps the reader to understand the numbers without having to recalculate from log-values.

In Fig 4E-F, what does the vertical lines mean? Please explain.

Some isssues about the text:

The writing of the introduction can be improved. Perhaps send this to some editorial service.

R49: please explain 'technological packages' or preferably state what you mean.
R53: Never leave 'this' alone as the interpretation is then ambiguous.
R69-70: No need to refer to the same paper in two places in the same sentence.
R76-78: Awkward formulation, please change.
R79-84: You repeat information already presented in the paragraph. Please rewrite the whole paragraph.
R85: How important is the spider life cycle. You only seem to suggest that variability arises because of difference in the cropping systems, but variation in spider abundance is also strongly dependent on the breeding period for different spider species.
R91-97: Very long sentence. Please break up.
R97-99: Unclear sentence. Please clarify.
R113: There is very high variability in the dispersal capacity and most ground- and vegetation hunters also use ballooning during the juvenile stages. For spider traits, check Bell et al. 2005. Bull Ent Res. 95:69-114
R152: I assume that you mean 2,300 kg and not 2.3 kg
R170: Is the design additive or substitutive?
R276: Why use poisson and negative-binomial for richness estimates? These are often normally distributed.
R315: Again, Pachgnatha are not web-builders. And I assume that the table should be S.1

This paper can be a nice contribution if you fix these issues.

Reviewer: 3

Referees Comments
The authors' approach is interesting, demonstrating that crop diversification generates greater abundance and richness of spiders, together with the stages of the agricultural cycle. It is recommended to review the following bibliography for line 432:
Benamú, M. & Viera, C. 2023. PRESENCE OF SPIDERS IN STRATA OF LEMON TREES (CITRUS LIMON), MONTEVIDEO, URUGUAY. In book: Agroecologia: produção e sustentabilidade em pesquisa - Volume 3

[email ref: DL-SW-3-a]

Agricultural and Forest Entomology

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

Journal:	*Agricultural and Forest Entomology*
Manuscript ID	Draft
Wiley - Manuscript type:	Original Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Quijano Cuervo, Luis; Instituto de Ecologia, Red de Ecología Funcional del Val, Ek; UNAM IIES Macias Ordoñez, Rogelio; Instituto de Ecologia, Ecología Evolutiva Dáttilo, Wesley; Instituto de Ecologia, Red de Ecoetología Negrete Yankelevich, Simoneta; Instituto de Ecologia
Keywords:	guilds, local management, forest, dispersal, temporal variation
Abstract:	1. Agroecosystem simplification for 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 diversity 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. 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.

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

Luis G. Quijano-Cuervo[a], Ek del-Val[b], Rogelio Macías-Ordóñez[c], Wesley Dáttilo[d], Simoneta Negrete-Yankelevich[a*]

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Abstract

1. Agroecosystem simplification for 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 diversity 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.

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.

Introduction

The introduction of technological packages to increase food production has promoted the loss of biodiversity in agricultural crops (Altieri & Trujillo, 1987; Lichtenberg et al., 2017). This reduction in agrodiversity has led to the loss of ecosystem services such as natural pest control by natural predators (Altieri & Trujillo, 1987; Gallé et al., 2019). This is of utmost importance since it is estimated that global crop productivity can decrease up to 40% due to damage caused by pest insects (FAO, 2021). Polycultures based on traditional systems such as "*milpas*" (*i.e.* polyculture with maize, beans, and squash as main crops; Zizumbo et al., 2012) can be a viable alternative to improve the biodiversity of agricultural fields (Altieri & Trujillo, 1987; Isakson, 2009) since these systems maintain a relatively high diversity of plants due to the mixture of cultivated (and promoted) species, and have a limited use of inputs such as pesticides which can be detrimental to predators (Birkhofer et al., 2013). However, predators such as spiders have complex responses to factors that shape their abundance and diversity in agricultural crops (Birkhofer et al., 2013). Thus, to create adequate management strategies that promote taxonomically and functionally diverse communities that would help in natural pest control, it is necessary to have a better understanding of what determines the dynamics of spider communities in polycultures.

Agroecological management has been proposed as an alternative for sustainable agriculture while maintaining crop biodiversity (Wezel et al., 2014; Martínez-Camacho et al., 2022). Crop diversification by including plant species that increase plant heterogeneity and prey availability (Sunderland & Samu, 2000) is an agroecological practice used to promote high spider richness and abundance (Sunderland & Samu, 2000; 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 (*i.e.* natural and semi-natural habitat areas) surrounding the crops (Batáry et al., 2011; Galloway et al., 2021). For example, Galloway et al., (2021) showed that spider richness and abundance only responded positively to agroecological management in perennial crops surrounded by simplified landscapes (*i.e.* little forest cover). In 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 different regional sources of organisms (Batáry et al., 2011). These findings emphasize the importance of taking into account the interaction between local crop management and the surrounding landscape (Galloway et al., 2021; Schmidt et al., 2005), since the success of implementing practices such as plant diversification to increase predator abundance and the contribution to pest control may depend on the context of the landscape where the cultivation plots are established (Batáry et al., 2011).

In annual crops, there is high temporal variation related to the intra-annual dynamics of agricultural practices (*e.g.* plowing), weather conditions, and vegetation (Kennedy & Storer, 2000). This intra-annual variation produces a temporal dynamic in spider communities, where there is higher 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). In this sense, the importance of agroecological practices that increase the availability of shelters and prey for spiders in annual crops, such as plant diversification, depends on the stage of the agricultural cycle, and a stronger positive effect on spider diversity is expected in stages with greater disturbance to spider communities such as winter, which is when most crops are harvested and there is extreme weather (Gavish-Regev et al., 2008; Sunderland & Samu, 2000). Furthermore, given that spiders are dispersed among habitats in agrolandscapes avoiding extreme weather, searching for prey, or avoiding direct death by practices like plowing (Birkhofer et al., 2013; Gavish-Regev et al., 2008), the effect of a higher number of natural habitats (*e.g*. forest areas) is also likely to be more important in stages of the agricultural cycle with greater disturbance (Schmidt et al., 2008, 2005; Schmidt & Tscharntke, 2005; Triquet et al., 2022). Most studies consider that the effect of local management and the surrounding landscape on spiders in agricultural crops is static (Birkhofer et al., 2013; Lichtenberg et al., 2017). However, it is necessary to consider that the temporal dynamics of spiders likely results in the effect of local management also depending on the stages of the agricultural cycle where it is applied (Schmidt et al., 2005; Schmidt & Tscharntke, 2005). This would partly explain why some studies have not detected clear positive effects of increasing the heterogeneity of the local vegetation and the landscape 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). Given that some groups of spiders with high dispersal capacity (*e.g. web-building spiders*, 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), guilds that disperse only a few meters or kilometers by walking (*e.g. ground* and *vegetation hunters,* 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.

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 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).

Spider community sampling and taxonomic identification

Spider sampling was performed with three capture methods commonly used to catch these predators (Ubick et al., 2005), 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* (GH), *vegetation hunters* (VH), and *web-builders* (WE). 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. *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*), 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 Tetragnathidae (*Pachygnatha* sp1, 23%) (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 (β_{slope} = 0.69) and in the *ground hunter* (β_{slope} = 1.11) and *vegetation hunter* (β_{slope} = 0.32) guilds (Table 1, Figures 3 and 4). The richness of the entire community (β_{slope} = 0.13) and of *vegetation hunters* (β_{slope} = 0.24) was also positively associated with the forest area surrounding the crop plots (Figure 4C-D). 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 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).

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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References

Altieri, M.A. & Trujillo, J. (1987) The agroecology of corn production in Tlaxcala, Mexico. *Human Ecology*, 15, 189–220.

Amaral, D.S.S.L., Venzon, M., Santos, H.H. dos, Sujii, E.R., Schmidt, J.M. & Harwood, J.D. (2016) Non-crop plant communities conserve spider populations in chili pepper agroecosystems. *Biological Control*, 103, 69–77.

Batáry, P., Báldi, A., Kleijn, D. & Tscharntke, T. (2011) Landscape-moderated biodiversity effects of agri-environmental management: A meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, 278, 1894–1902.

Beaumelle, L., Auriol, A., Grasset, M., Pavy, A., Thiéry, D. & Rusch, A. (2021) Benefits of increased cover crop diversity for predators and biological pest control depend on the landscape context. *Ecological Solutions and Evidence*, 2, 1–12.

Benamú, M.A., Lacava, M., García, L.F., Santana, M. & Viera, C. (2017) Spiders associated with agroecosystems: Roles and perspectives. In: *Behaviour and Ecology of Spiders: Contributions from the Neotropical Region*. Springer International Publishing, pp. 275–302.

Birkhofer, K., Entling, M.H. & Lubin, Y. (2013) Agroecology: Trait composition, spatial relationships, trophic interactions. In: Penney, D. (Ed.) *Spider Research in the 21st Century trends & perspectives*. Siri Scientific Press, Manchester, pp. 200–229.

Burnham, K.P. & Anderson, D.R. (2002) Model Selection and Multimodel Inference, 2nd ed. Springer.

Cardoso, P., Pekár, S., Jocqué, R. & Coddington, J.A. (2011) Global patterns of guild composition and functional diversity of spiders. *PLoS ONE*, 6, 1–10.

Carvalho, J.C. & Cardoso, P. (2014) Drivers of beta diversity in Macaronesian spiders in relation to dispersal ability. *Journal of Biogeography*, 41, 1859–1870.

Coll, M. & Bottrell, D. (1995) Predator-prey association in mono- and dicultures: Effect of maize and bean vegetation. *Agriculture, Ecosystems & Environment*, 54, 115–125.

Dassou, A.G. & Tixier, P. (2016) Response of pest control by generalist predators to local-scale plant diversity: A meta-analysis. *Ecology and Evolution*, 6, 1143–1153.

Dauber, J., Purtauf, T., Allspach, A., Frisch, J., Voigtländer, K. & Wolters, V. (2005) Local vs. landscape controls on diversity: A test using surface-dwelling soil macroinvertebrates of differing mobility. *Global Ecology and Biogeography*, 14, 213–221.

Denys, C. & Tscharntke, T. (2002) Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. *Oecologia*, 130, 315–324.

Feber, R.E., Johnson, P.J., Bell, J.R., Chamberlain, D.E., Firbank, L.G., Fuller, R.J., et al. (2015) Organic farming: Biodiversity impacts can depend on dispersal characteristics and landscape context. *PLoS ONE*, 10, 1–20.

Gallé, R., Happe, A.K., Baillod, A.B., Tscharntke, T. & Batáry, P. (2019) Landscape configuration, organic management, and within-field position drive functional diversity of spiders and carabids. *Journal of Applied Ecology*, 56, 63–72.

Galloway, A.D., Seymour, C.L., Gaigher, R. & Pryke, J.S. (2021) Organic farming promotes arthropod predators, but this depends on neighboring patches of natural vegetation. *Agriculture, Ecosystems and Environment*, 310, 107295.

Gavish-Regev, E., Lubin, Y. & Coll, M. (2008) Migration patterns and functional groups of spiders in a desert agroecosystem. *Ecological Entomology*, 33, 202–212.

Geldenhuys, M., Gaigher, R., Pryke, J.S. & Samways, M.J. (2021) Diverse herbaceous cover crops promote vineyard arthropod diversity across different management regimes. *Agriculture, Ecosystems and Environment*, 307, 107222.

Gliessman, S.R. (2015) Agroecology The Ecology of Sustainable Food Systems, 3rd ed. CRC Press.

Gonthier, D.J., Ennis, K.K., Farinas, S., Hsieh, H.Y., Iverson, A.L., Batáry, P., et al. (2014) Biodiversity conservation in agriculture requires a multi-scale approach. *Proceedings of the Royal Society B: Biological Sciences*, 281, 9–14.

Isakson, S.R. (2009) No hay ganancia en la milpa: The agrarian question, food sovereignty, and the on-farm conservation of agrobiodiversity in the Guatemalan highlands. *Journal of Peasant Studies*, 36, 725–759.

Jackson, H.B. & Fahrig, L. (2015) Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography*, 24, 52–63.

Jiménez-Valverde, A. & Lobo, J.M. (2005) Determining a Combined Sampling Procedure for a Reliable Estimation of Araneidae and Thomisidae Assemblages (Arachnida, Araneae). *Journal of Arachnology*, 33, 33–42.

Kennedy, G.G. & Storer, N.P. (2000) Life systems of polyphagous arthropod pests in temporally unstable cropping systems. *Annual Review of Entomology*, 45, 467–493.

Landis, D.A., Menalled, F.D., Costamagna, A.C. & Wilkinson, T.K. (2005) Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. *Weed Science*, 53, 902–908.

Letourneau, D.K. (1986) Associational Resistance in Squash Monocultures and Polycultures in Tropical Mexico. *Environmental Entomology*, 15, 285–292.

Letourneau, D.K. (1987) The Enemies Hypothesis: Tritrophic Interactions and Vegetational Diversity in Tropical Agroecosystems. *Ecology*, 68, 1616–1622.

Letourneau, D.K. (1990) Mechanisms of predator accumulation in a mixed crop system. *Ecological Entomology*, 15, 63–69.

Letourneau, D.K., Jedlicka, J.A., Bothwell, S.G. & Moreno, C.R. (2009) Effects of Natural Enemy Biodiversity on the Suppression of Arthropod Herbivores in Terrestrial Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 40, 573–592.

Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., et al. (2017) A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Global Change Biology*, 23, 4946–4957.

Martínez-Camacho, Y.D., Negrete-Yankelevich, S., Maldonado-Mendoza, I.E., Núñez-de la Mora, A. & Amescua-Villela, G. (2022) Agroecological management with intra- and interspecific diversification as an alternative to conventional soil nutrient management in family maize farming. *Agroecology and Sustainable Food Systems*, 46, 364–391.

Méndez-Castro, F.E., Mendieta-Leiva, G., Rao, D. & Bader, M.Y. (2020) Island-biogeographic patterns of spider communities on epiphytes depend on differential space use among functional groups. *Journal of Biogeography*, 47, 1322–1332.

Michalko, R. & Košulič, O. (2019) The management type used in plum orchards alters the functional community structure of arthropod predators. *International Journal of Pest Management*, 66, 173-181.

Michalko, R. & Pekár, S. (2016) Different hunting strategies of generalist predators result in functional differences. *Oecologia*, 181, 1187–1197.

Michalko, R., Pekár, S. & Entling, M.H. (2019) An updated perspective on spiders as generalist predators in biological control. *Oecologia*, 189, 21-36.

Midega, C.A.O., Khan, Z.R., Berg, J. Van Den, Ogol, C.K.P.O., Dippenaar-Schoeman, A.S., Pickett, J.A., et al. (2008) Response of ground-dwelling arthropods to a “push-pull” habitat management system: Spiders as an indicator group. *Journal of Applied Entomology*, 132, 248–254.

Negrete-Yankelevich, S. & Fox, G.A. (2015) Spatial variation and linear modeling of ecological data. In: Fox, G.A., Negrete-Yankelevich, S. & Sosa, V.J. (Eds.) Ecological statistics: contemporary theory and application. Oxford University Press, Oxford, United Kingdom, pp. 228–260.

Nivedita Priyadarshini, K., Kumar, M., Rahaman, S.A. & Nitheshnirmal, S. (2018) a Comparative Study of Advanced Land Use/Land Cover Classification Algorithms Using Sentinel-2 Data. *The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences*, XLII–5, 665–670.

Nyffeler, M. & Benz, G. (1988) Feeding ecology and predatory importance of wolf spiders (Pardosa spp.) (Araneae, Lycosidae) in winter wheat fields. *Journal of Applied Entomology*, 106, 123–134.

Pearce, S., Zalucki, M.P. & Hassan, E. (2005) Spider ballooning in soybean and non-crop areas of southeast Queensland. Agriculture, *Ecosystems and Environment*, 105, 273–281.

Picchi, M.S. (2020) Spiders (Araneae) of olive groves and adjacent semi-natural habitats from central Italy. *Arachnologische Mitteilungen*, 60, 1–11.

Picchi, M.S., Bocci, G., Petacchi, R. & Entling, M.H. (2016) Effects of local and landscape factors on spiders and olive fruit flies. *Agriculture, Ecosystems and Environment*, 222, 138–147.

Poveda, K., Gómez, M.I. & Martínez, E. (2008) Diversification practices: Their effect on pest regulation and production. *Revista Colombiana de Entomología*, 34, 131–144.

Quijano-Cuervo, L.G., Rao, D., Escobar Sarria, F., Dáttilo, W. & Negrete-Yankelevich, S. (2022) Shade tree isolation in pastures modulates diversity of epiphyte-dwelling spiders: The role of epiphyte biomass and species dispersal capacity. *Insect Conservation and Diversity*, 15, 682-692.

Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G. & Ekbom, B. (2014) Management intensity at field and landscape levels affects the structure of generalist predator communities. *Oecologia*, 175, 971–983.

Rypstra, A.L., Carter, P.E., Balfour, R.A. & Marshall, S.D. (1999) Architectural features of agricultural habitats and their impact on the spider inhabitants. *Journal of Arachnology*, 27, 371–377.

Salman, I.N.A., Gavish-Regev, E., Saltz, D. & Lubin, Y. (2019) The agricultural landscape matters: spider diversity and abundance in pomegranate orchards as a case study. *BioControl*, 64, 583–593.

Schmidt-Entling, M.H. & Döbeli, J. (2009) Sown wildflower areas to enhance spiders in arable fields. *Agriculture, Ecosystems and Environment*, 133, 19–22.

Schmidt, M.H., Roschewitz, I., Thies, C. & Tscharntke, T. (2005) Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *Journal of Applied Ecology*, 42, 281–287.

Schmidt, M.H., Thies, C., Nentwig, W. & Tscharntke, T. (2008) Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *Journal of Biogeography*, 35, 157–166.

Schmidt, M.H. & Tscharntke, T. (2005) Landscape context of sheetweb spider (Araneae: Linyphiidae) abundance in cereal fields. *Journal of Biogeography*, 32, 467–473.

Sørensen, L.L., Coddington, J. a. & Scharff, N. (2002) Inventorying and Estimating Subcanopy Spider Diversity Using Semiquantitative Sampling Methods in an Afromontane Forest. *Environmental Entomology*, 31, 319–330.

Sunderland, K. & Samu, F. (2000) Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: A review. *Entomologia Experimentalis et Applicata*, 95, 1-13.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., et al. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31, 79–92.

Thomas, C.F.G., Brain, P. & Jepson, P.C. (2003) Aerial activity of linyphiid spiders: Modelling dispersal distances from meteorology and behaviour. *Journal of Applied Ecology*, 40, 912–927.

Triquet, C., Roume, A., Tolon, V. & Wezel, A. (2022) Undestroyed winter cover crop strip in maize fields supports ground-dwelling arthropods and predation. *Agriculture, Ecosystems and Environment*, 326, 107783.

Ubick, D., Paquin, P., Cushing, P.E. & Roth, V. (2005) Spiders of North America: an identification manual. American Arachnological Society.

Wezel, A., Casagrande, M., Celette, F., Vian, J.F., Ferrer, A. & Peigné, J. (2014) Agroecological practices for sustainable agriculture. A review. *Agronomy for Sustainable Development*, 34, 1–20.

Wu, L., Si, X., Didham, R.K., Ge, D. & Ding, P. (2017) Dispersal modality determines the relative partitioning of beta diversity in spider assemblages on subtropical land-bridge islands. *Journal of Biogeography*, 44, 2121–2131.

Zizumbo, D., Flores, A. & Colunga, P. (2012) The Archaic Diet in Mesoamerica: Incentive for Milpa Development and Species Domestication 1. *Economic Botany*, 66, 328–343.

Zuckerberg, B., Cohen, J.M., Nunes, L.A., Bernath-Plaisted, J., Clare, J.D.J., Gilbert, N.A., et al. (2020) A Review of Overlapping Landscapes: Pseudoreplication or a Red Herring in Landscape Ecology? *Current Landscape Ecology Reports*, 5, 140–148.

Figures and tables

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	***Abundance*** ***(Ln [No. Ind. · plot^{-1}])***	ni	ni	Winter (0.76) Planting (0.61) Growth (2.31) Fructification (2.09) Harvest (1.83)	256.7	278.7 (21.9)	281.1 (24.3)
	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 AIC_{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.

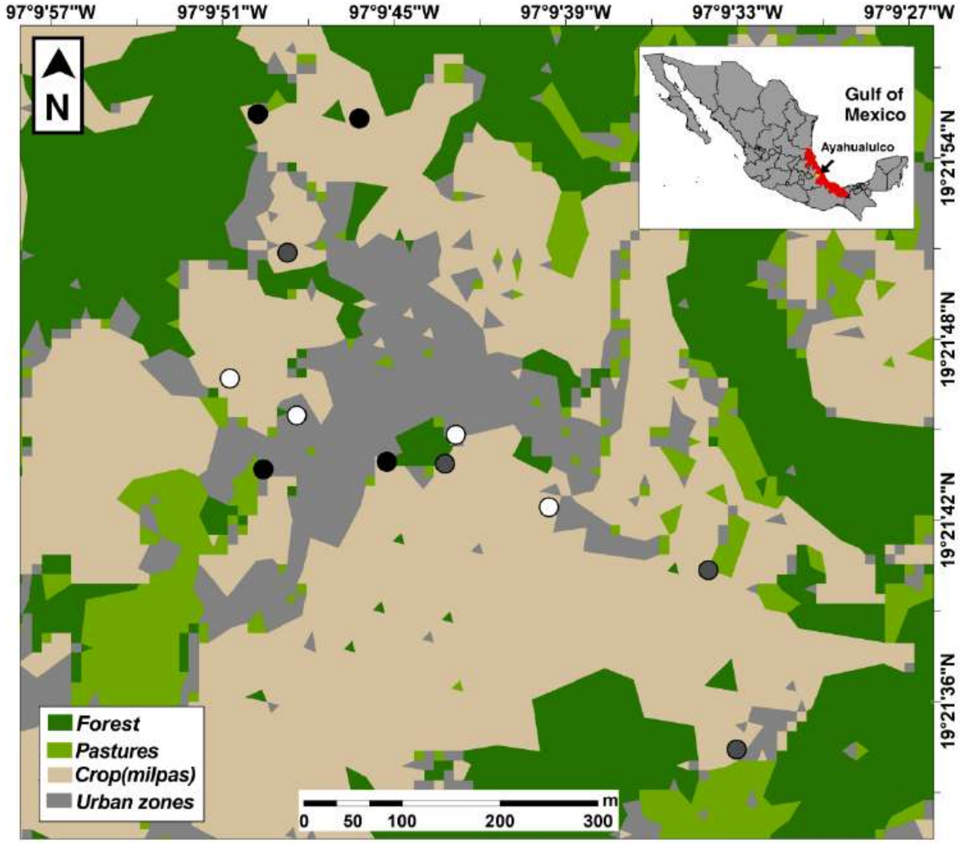

Figure 1. Study area location and map of the main land uses. Land uses were generated from the supervised classification of a Sentinel image (10-meter resolution). Colors: black= plots with the basic triad Maize-Bean-Squash (M-B-S), dark grey= plots with the basic triad and added legumes (M-B-S + L),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

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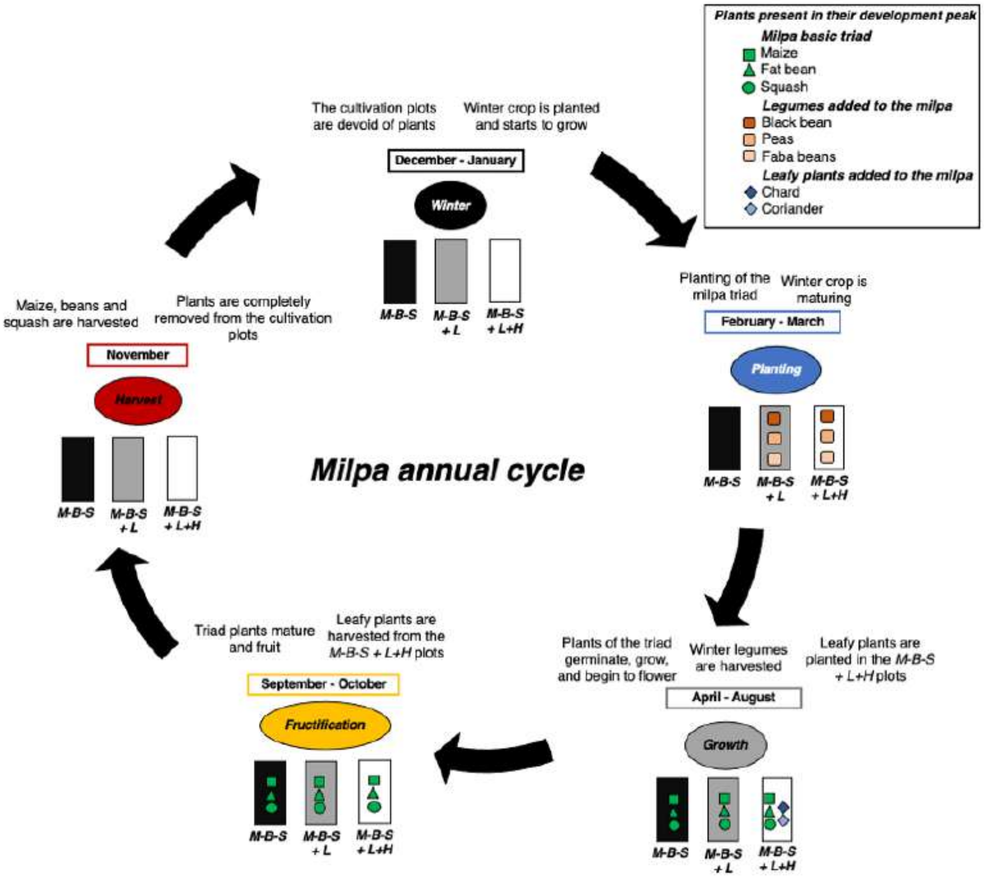

Figure 2. Summary of the stages of the milpa agricultural cycle. The stages were divided based on the most important events during the months of crop development. Note that the presence of some plant species in certain stages depends on the level of plant diversification. Abbreviations: M-B-S = plots 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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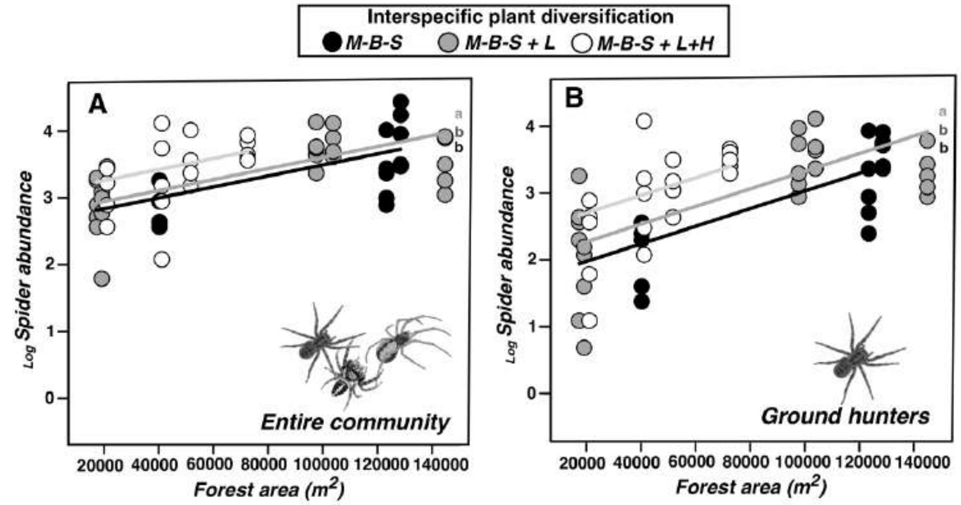

Figure 3. Effect of plant diversification and the surrounding landscape on the abundance of the entire spider community and ground-hunting spiders. M-B-S = plots with the basic triad Maize-Bean-Squash, M-B-S + L = plots with the basic triad and additional legumes, M-B-S + L+H = plots with the basic triad,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

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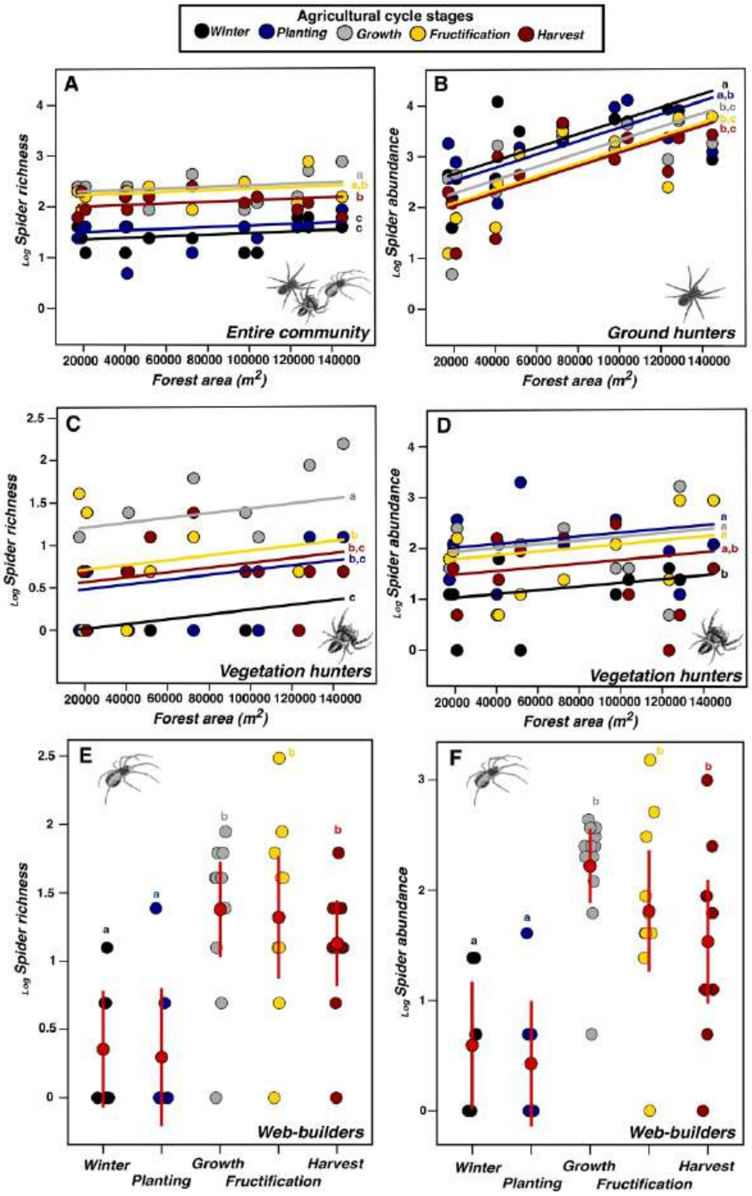

Figure 4. Effect of the milpa agricultural cycle and the landscape on the richness and abundance of the entire spider community and the spider guilds. Different letters to the right of the fitted lines indicate significant differences between the intercepts. Note that abundance and richness values (# of individuals and species) are expressed as logarithms, and we plotted different trendlines with different intercepts but with the same slopes.

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BIODIVERSIDAD DE ARAÑAS EN CAFETALES Y MILPAS AGROECOLÓGICAS: INTEGRANDO LA DESCRIPCIÓN DE NUEVAS ESPECIES Y EL ESTUDIO DE LOS PATRONES Y PROCESOS ECOLÓGICOS

TESIS QUE PRESENTA LUIS G. QUIJANO CUERVO

PARA OBTENER EL GRADO DE **DOCTOR EN CIENCIAS**

XALAPA, VERACRUZ, MÉXICO 2023

INECOL
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TABLA DE CONTENIDO

TABLA DE CONTENIDO FIGURAS Y CUADROS

CAPÍTULO 3. DIVERSIDAD DE ARAÑAS TEJEDORAS Y CAZADORAS DEL FOLLAJE EN CULTIVOS MIXTOS Y MONOCULTIVOS DE MAÍZ Y FRIJOL: *UN ENFOQUE EXPERIMENTAL*

Diversidad de arañas tejedoras y cazadoras del follaje en cultivos mixtos y monocultivos de maíz y frijol: *un enfoque experimental*

Resumen

La diversificación local o regional de los cultivos lograda a partir de plantar y mezclar diversas especies vegetales, beneficia la presencia de depredadores naturales como las arañas. No obstante, todavía no se tiene una comprensión integradora sobre los efectos de la diversificación vegetal (*e.g. aditivo*, *sinérgico* o *negativo*) en las arañas de los diferentes gremios tróficos. Aquí, a través de un experimento en campo realizado en un agropaisaje de *milpas* en México, estudiamos cómo la riqueza y abundancia de arañas y la diversidad beta (cambio en la composición de especies) de los dos principales gremios de arañas de la vegetación (*arañas cazadoras* y *tejedoras*) diferían entre monocultivos y dicultivos de maíz y frijol, y sus estratos vegetales (plantas del cultivo vs herbáceas). Además, analizamos el aporte de las diferentes escalas espaciales involucradas en el experimento (*i.e.* unidades, estratos o parcelas en el paisaje) a la diversidad regional de arañas. Encontramos que la mezcla de leguminosas con plantas de maíz en forma de dicultivo propicia comunidades de arañas más abundantes en comparación con monocultivos de maíz o frijol. También, encontramos que la riqueza y abundancia de arañas difiere entre los estratos dentro de los cultivos y que la diversidad regional de arañas está mayormente explicada por una alta diversidad beta entre los tipos de cultivos. Nuestro estudio ofrece nueva evidencia empírica y experimental que apoya la ventaja de tener diferentes cultivos mezclados con el fin de propiciar comunidades de arañas más abundantes que en los monocultivos. Esta mezcla tradicional de diferentes cultivos y estratos vegetales en el caso de la *milpa*, tiene la ventaja de crear ensambles de arañas locales y regionales diversos que pueden tener un mejor aporte al control natural de herbívoros que dañan y reducen el rendimiento de los cultivos.

Palabras clave: monocultivos, policultivos, gremios de arañas, herbáceas, diversificación intercalada, *milpa*.

1. Introducción

La intensificación de la producción agrícola producto de la alta demanda de alimento ha promovido la simplificación de los paisajes agrícolas, en los cuales predominan grandes áreas de monocultivo y pequeños remanentes de vegetación perenne (Altieri y Nicholls, 2004; Bianchi et al., 2006). Se estima que en los últimos 30 años se han perdido en el mundo ≈*180 mil ha* de bosque y se han aumentado en ≈*76 mil ha* las tierras de cultivo, en su mayoría monocultivos (FAO, 2023). Esta simplificación de los agropaisajes ha promovido la disminución de la biodiversidad de los cultivos (Bianchi et al., 2006; Paredes et al., 2021), y con ello la pérdida de servicios ecosistémicos importantes para su funcionamiento como el control natural de plagas (Altieri y Nicholls, 2004). Actualmente, una creciente consciencia de los perjuicios económicos, ecológicos y a la salud, que conlleva la pérdida de la biodiversidad de los campos agrícolas ha impulsado la búsqueda de estrategias alternativas a la agricultura convencional que muchas veces implican retomar prácticas ancestrales de cultivo (Altieri y Nicholls, 2004; Gliessman, 2015).

Prácticas agroecológicas como la diversificación vegetal tienen el potencial de ayudar a mitigar la pérdida de la biodiversidad que los campos agrícolas albergan (Lichtenberg et al., 2017). La diversificación intercalada lograda a partir de plantar diversas especies de cultivo o promoviendo el crecimiento de plantas no cultivadas en diferentes estratos (Poveda et al., 2008; Samu et al., 1999), beneficia la presencia de depredadores naturales como las arañas (Sunderland y Samu, 2000). Este aumento en la heterogeneidad vegetal de los cultivos aumenta la cantidad de hábitats y presas para las arañas (Tews et al., 2004), lo cual promueve un incremento hasta de un 80% en su diversidad (abundancia o riqueza de especies, Samu *et al.* 1999, Sunderland y Samu 2000). Dependiendo de las interacciones que ocurran entre las arañas, otros depredadores, presas, y las plantas hospederas, se pueden esperar diferentes efectos de la diversificación vegetal sobre la diversidad de arañas (*i.e. aditivo*, *sinérgico* o *negativo*, Poveda *et al*. 2008, Riechert y Bishop 1990, Sunderland y Samu 2000). Un efecto aditivo de la diversificación de cultivos sobre la diversidad de arañas (*i.e*. aumento del doble de la diversidad de los monocultivos), podría ocurrir cuando las diferentes especies de arañas encuentran hábitats adecuados y recursos alimentarios específicos en cada tipo de cultivo permitiéndoles coexistir en un mismo campo (Letourneau, 1990; Sunderland y Samu, 2000). Por otro lado, un efecto sinérgico (*i.e*. aumento de más del doble de la diversidad de los monocultivos) podría ocurrir cuando las interacciones positivas entre las especies de arañas (facilitación) y las plantas (mutualismo) en los cultivos mezclados generan beneficios mutuos, como una mayor disponibilidad de hábitats y recursos alimentarios, promoviendo la coexistencia de arañas en todas las plantas del campo y aumentando la diversidad (Coll y Bottrell, 1995; Sunderland y Samu, 2000). Por último, es posible que se presente un efecto negativo en el que las interacciones antagonistas como la competencia, depredación o la dominancia de una especie sobre otra (Letourneau et al., 2009; Michalko et al., 2021), probablemente lleven a una disminución en la diversidad de arañas en los cultivos mezclados en comparación con los monocultivos (Poveda et al., 2008). A pesar de conocerse la relación entre la diversificación vegetal intercalada de los cultivos y la diversidad de arañas (*revisado por* Sunderland y Samu, 2000), todavía se carece de evidencia empírica y experimental sobre los efectos en especies con diferentes dominancias ecológicas, estrategias de caza o grado de asociación variable con las plantas del cultivo o estratos vegetales (*i.e. gremios*, Birkhofer et al., 2013; Uetz et al.,1999).

Los policultivos tradicionalmente diversificados como las *milpas* son sistemas donde crecen intercaladamente diferentes especies de plantas cultivables (principalmente maíz, frijol y calabaza) y silvestres (herbáceas estacionales) (Altieri y Trujillo, 1987), y en comparación con los monocultivos estos albergan una mayor riqueza y abundancia de arañas (Coll y Bottrell, 1995). La diversificación en estos sistemas regularmente ocurre a escala de parcela (Fonteyne et al., 2023; Poveda et al., 2008). Sin embargo, el aumento de la heterogeneidad en los estratos vegetales o el paisaje, podrían aportar de diferente manera a la diversidad regional de arañas (Poveda et al., 2008; Sunderland y Samu, 2000; Wezel et al., 2014), e identificar cuál escala es la de mayor relevancia para su manejo es de suma importancia (Tscharntke et al., 2007). Sin embargo, este es un tema que poco se ha explorado en los sistemas agrícolas y que amerita mayor evidencia empírica (Escobar-Ramírez et al., 2020; Gering et al., 2003). Previamente se ha demostrado que la diversificación de cultivos de maíz con leguminosas crea nuevos microhábitats que promueven un aumento en la diversidad de arañas al interior de las parcelas (Coll y Bottrell, 1995), particularmente de especies con preferencia por las plantas principales del cultivo (*arañas cazadoras*, Armendano y González, 2011; Benamú et al., 2017). Se sabe que las *arañas tejedoras* están asociadas con vegetación que les permite la sujeción de sus telas como plantas con numerosos tallos, hojas erectas y agrupadas (*e.g.* plantas de frijol o herbáceas) (Hesselberg et al., 2023), mientras que las *arañas cazadoras* ocurren con mayor frecuencia en plantas con hojas arqueadas y muy espaciadas (*e.g.* plantas de maíz, Stuntz et al., 2002). Es probable que la mezcla de plantas con diferentes formas de crecimiento (*e.g.* leguminosas y plantas de maíz) y estratos vegetales (*e.g* herbáceas y plantas del cultivo), induzca la mezcla de ensambles con preferencia por las diferentes especies vegetales y esto provoque el aumento en la diversidad de arañas (Coll y Bottrell, 1995). Identificar el tipo de efecto que tiene la mezcla tradicional de cultivos en la diversidad de arañas de las milpas (*aditivo*, *sinérgico* o *negativo*) es de suma importancia debido al potencial de estos depredadores para el control natural de las plagas que afectan los cultivos de maíz (Blanco et al., 2014).

En el presente estudio, a través de un experimento en campo realizado en un agropaisaje de *milpas* en México, estudiamos cómo la riqueza, abundancia y diversidad beta (cambios en la composición de especies) de los dos principales gremios de arañas de la vegetación (*arañas cazadoras* y *tejedoras*) diferían entre monocultivos y dicultivos compuestos por maíz y frijol. Adicionalmente, permitimos el crecimiento de herbáceas en las parcelas experimentales, y comparamos la diversidad entre el estrato herbáceo no cultivado y las plantas de los cultivos, y además analizamos su aporte a la diversidad regional de arañas. Debido a que se espera que cada cultivo (maíz vs. frijol) tenga una fauna de arañas característica, (1) esperábamos una alta diversidad beta de arañas entre los diferentes monocultivos, (2) y que esto provocara que al mezclar los cultivos se promoviera un aumento en la diversidad alfa de arañas de los dicultivos, igual o mayor a la suma de la diversidad de los monocultivos (Sunderland y Samu, 2000). Esperábamos que el aumento de la diversidad alfa fuera mayor para el grupo de las *arañas cazadoras*, las cuales están mayormente asociadas a las plantas de maíz (Armendano y González, 2011). Con relación a los estratos, (3) esperábamos diferencias en la composición de arañas de ambos gremios entre las herbáceas no cultivadas y las plantas del cultivo, y que, (4) para el caso de las *arañas tejedoras* estás tuvieran una mayor diversidad de especies en el estrato herbáceo no cultivado (Benamú et al., 2017). Por último, (5) esperábamos que la variación en la diversidad beta de arañas fuera mayor entre los tipos de cultivos (*e.g.* maíz vs. frijol), que entre los estratos o unidades de estudio dentro de las parcelas.

2. Métodos

2.1 Área de estudio

Este estudio fue desarrollado en una zona de alrededor de la comunidad de Ocotepec, Veracruz, México (19°21'38.24" N, 97° 9'41.78" W). El paisaje del área de estudio está dominado en su mayoría por grandes zonas de cultivo de maíz de temporal (en su forma de policultivo tradicional con frijol y calabaza denominando *milpa*), pastizales/arbustos (zonas con pastos y especies de arbustos, en su mayoría *Baccharis conferta* Kunth), pocos remanentes de bosque natural y algunas zonas de cultivo de pino. Las milpas sembradas en el área de estudio son exclusivamente para la alimentación familiar, su manejo es convencional (con uso de fertilizantes químicos y arado) y el rendimiento de grano de maíz alcanza aproximadamente 2,300 $kg \cdot ha^{-1}$ (Martínez-Camacho et al., 2022). El ciclo agrícola en la zona va de marzo a noviembre y el maíz solo se cosecha una vez al año.

2.2 Parcelas experimentales de monocultivos y dicultivos de maíz y frijol

Para este estudio seleccionamos 12 parcelas (20 m x 10 m) pertenecientes a voluntarios en el proyecto *Mano Vuelta*, cuyo objetivo es mejorar la sostenibilidad de la producción de alimentos para las familias rurales de la región (Martínez-Camacho et al., 2022). Estas parcelas han recibido un manejo de tipo agroecológico por lo menos durante 6 años previo al estudio, el cual consta de la suspensión total de la labranza y una fertilización orgánica con un fertilizante (*bokashi*) elaborado *in situ* con rastrojo, estiércol de oveja, ceniza, pulque (bebida de agave fermentada localmente como fuente de microorganismos), tierra y azúcar morena sin refinar (Martínez-Camacho et al., 2022).

Para nuestro experimento, de las 12 parcelas disponibles cuatro de ellas fueron seleccionadas para sembrar una mezcla de plantas de maíz y frijol como tradicionalmente se hace en la región (*dicultivo*), otras cuatro parcelas fueron sembradas solo con maíz (*Zea mays* L.) y las otras cuatro con una especie de frijol común de la zona (*Phaseolus coccineus* L.) (monocultivos). No incluimos el chilacayote (*Cucurbita ficifolia* Bouché) al experimento debido a que este representa un cultivo secundario en la región de estudio, además de que es difícil controlar su densidad dentro de las parcelas experimentales y porque regularmente no se encuentran arañas asociadas a esta planta (Quijano-Cuervo *obs. personal*). Nuestro experimento comenzó en marzo de 2022, en ese momento las parcelas fueron fertilizadas con *bokashi* y las semillas fueron sembradas. La siembra de cada especie se realizó como tradicionalmente lo hacen los agricultores en la zona, en surcos separados por un metro entre sí, para un aproximado de 10 surcos de 10 metros en cada parcela. En el caso de las parcelas con maíz y frijol, las semillas de ambas especies fueron sembradas en el hoyo. Durante los primeros dos meses se les pidió a los dueños de las parcelas extraer todas las plantas herbáceas con el fin de evitar que las plantas sembradas compitieran por luz, nutrientes o agua. Posterior a estos meses y cuando las plantas de los cultivos habían empezado a crecer, se dejaron crecer libremente todas las plantas herbáceas hasta que conformaron un estrato vegetal.

2.3 Muestreo e identificación taxonómica de las comunidades de arañas

Para el muestreo de las arañas utilizamos el método de agitación del follaje (Ubick et al., 2005), el cual estuvo dirigido a capturar las arañas de los dos principales estratos vegetales que se forman en las parcelas, el estrato asociado a las plantas del cultivo (0.30 m – 1.80 m) y el estrato formado por las herbáceas o malezas (0.0 m – 0.30 m). El muestro se hizo en 6 puntos, los cuales estaban ubicados en los extremos y el centro de las parcelas. En cada punto recolectamos las arañas en las herbáceas no cultivadas y las plantas de cultivo, con la ayuda de una red circular de 50 cm de diámetro y un madero que se usó para agitar la vegetación. Los ejemplares fueron recolectados durante 10 minutos por punto, con la ayuda de aspiradores bucales y pinzas, y preservados en frascos con alcohol etílico al 95%. Para evaluar la efectividad en la captura de arañas en cada tipo de cultivo y estrato vegetal, calculamos la cobertura de muestreo utilizando el estimador de cobertura de la muestra (Cn) propuesto por Chao y Jost (2012) (Cuadro 1). Las arañas adultas y juveniles se clasificaron en (morfo)especies según sus características morfológicas (somáticas y sexuales). Dado que algunos estadios juveniles son difíciles de asociar con una araña adulta, solo asignamos juveniles en estadios avanzados de desarrollo (subadultos) y que se encontraban en la misma unidad de muestreo donde se capturó el adulto. Cuando fue posible, los individuos se asignaron a una especie utilizando claves taxonómicas (Ubick et al., 2005; World Spider Catalog, 2021). Los individuos que no pudieron ser asignados a una especie fueron identificados como morfoespecies, los cuales fueron etiquetados con el nombre de la familia o género y un código alfanumérico (*e.g. Pachygnatha* sp1, *Anyphaena* sp1). Los códigos de las morfoespecies son exclusivos de este estudio. Para los análisis, utilizamos una clasificación de gremios tróficos en la cual las especies se agruparon en dos grupos de arañas típicas de la vegetación (Cardoso et al., 2011): *cazadoras* y *tejedoras*. Estos gremios difieren en su forma de acceder al alimento en la vegetación y grado de asociación con las plantas de los cultivos (*ver arriba*). Las *arañas cazadoras* usan refugios en la vegetación donde se reproducen, refugian, acechan y cazan activamente a sus presas; mientras que las arañas tejedoras en la mayoría de casos solo usan la vegetación como soporte para para construir sus telas y cazar pasivamente (Cardoso et al., 2011; Uetz et al., 1999).

2.4 Análisis de datos

2.4.1 Efecto del tipo de cultivo y el estrato sobre la riqueza, abundancia y composición de arañas

Evaluamos el efecto del tipo de cultivo (dicultivo [maíz + frijol], y monocultivo [maíz] [frijol]), el estrato (cultivo, herbáceas) y la interacción entre estos factores, sobre la riqueza y abundancia de los dos gremios de arañas a través de modelos lineales generalizados (GLM) con estructura de error *binomial negativo*. Para realizar los modelos usamos la función *glm* del paquete *stats* de R (R Core Team, 2022). Para elegir el *modelo mínimo adecuado* realizamos una selección automática de los modelos más probables y con menor AIC, esto con ayuda de la función *dredge* del paquete *MuMIn* (Bartoń, 2022) de R. Esta función escoge a partir de todas las combinaciones de modelos probables definidas a partir del modelo máximo (todas las variables y su interacción de segundo orden), aquellos modelos que tienen un mayor poder explicativo con un menor número de parámetros estimados. Elegimos como el modelo mínimo adecuado aquel con menor AIC, menor número de parámetros y que difería por lo menos en dos unidades de AIC con respecto a un modelo nulo (variable explicada por su media) (Burnham y Anderson, 2002). Para todos los modelos analizamos que los residuales cumplieran con los supuestos de normalidad, homocedasticidad y sobredispersión.

Con el fin de evaluar si la composición de especies de los dos gremios de arañas (*diversidad beta*) cambiaba con más frecuencia entre unidades (puntos de muestreo dentro de las parcelas), estratos dentro de las parcelas o tipos de cultivo, evaluamos la contribución de cada escala espacial a la diversidad regional de arañas (γ). Específicamente, utilizamos una partición aditiva de la diversidad, en la que $\gamma= \alpha+\beta_1+\beta_2+\beta_3$, donde γ es la riqueza total/regional de especies (registrada en todas las parcelas experimentales de estudio), α es la riqueza local de especies (unidades), β_1 es la diversidad beta entre unidades de muestreo, β_2 es la diversidad beta total entre estratos, β_3 es la diversidad beta entre tipos de cultivo (Crist et al., 2003; Jost et al., 2010). Probamos la significancia estadística del aporte de cada escala a la diversidad regional a través de comparar los valores observados de diversidad con los valores esperados bajo un modelo nulo construido con 999 aleatorizaciones (*ver* Crist et al., 2003). La hipótesis nula es que la diversidad media observada en cada escala es igual a la esperada por el modelo nulo, y esto debería ocurrir si la distribución de la diversidad es espacialmente homogénea (Antoniazzi et al., 2020). Realizamos la partición de la diversidad regional para las parcelas de los monocultivos y dicultivos, y también para las diferentes comparaciones de cultivos: frijol vs maíz, frijol vs dicultivos, maíz vs dicultivos. Por último, para comprender los procesos que regulan la variación espacial en la diversidad de arañas, separamos la diversidad beta de toda la comunidad en sus dos componentes: recambio (cambio de especies) y anidamiento (ganancia/pérdida de especies) (Baselga, 2010). Estos análisis fueron realizados en el software R usando las funciones *adipart* y *betapart* de los paquetes *vegan* (Oksanen et al., 2022) y *betapart* (Baselga et al., 2022).

3. Resultados

3.1 Dominancia de arañas en los estratos y tipos de cultivos

Tanto en los estratos como en los diferentes tipos de cultivo, la especie de *Pachygnatha* (*P. sp1*) perteneciente al gremio de arañas tejedoras, fue la araña con la mayor dominancia (número de individuos, Figura 1). En el estrato herbáceo, *Pachygnatha* sp1 aportó el 56% de la abundancia total, mientras que en el estrato asociado a las plantas de los cultivos esta araña fue dominante con el 46% de la abundancia total (Figura 1A-B). En el estrato de las plantas de los cultivos, *Anyphaena* sp1 fue la segunda especie de araña en dominancia con un aporte del 31% a la abundancia total (Figura 1A). *Pachygnatha* sp1 también fue la especie más dominante en los monocultivos de frijol (83 ind.) y maíz (81 ind.), a diferencia de los dicultivos (*Frijol* + *Maíz*) donde *Anyphaena* sp1 fue la especie más dominante en individuos (90 ind.) (Figura 1C-E, Cuadro 1). No hubo evidencia de un patrón de dominancia de alguno de los dos gremios por estratos o tipos de cultivo (Figura 1).

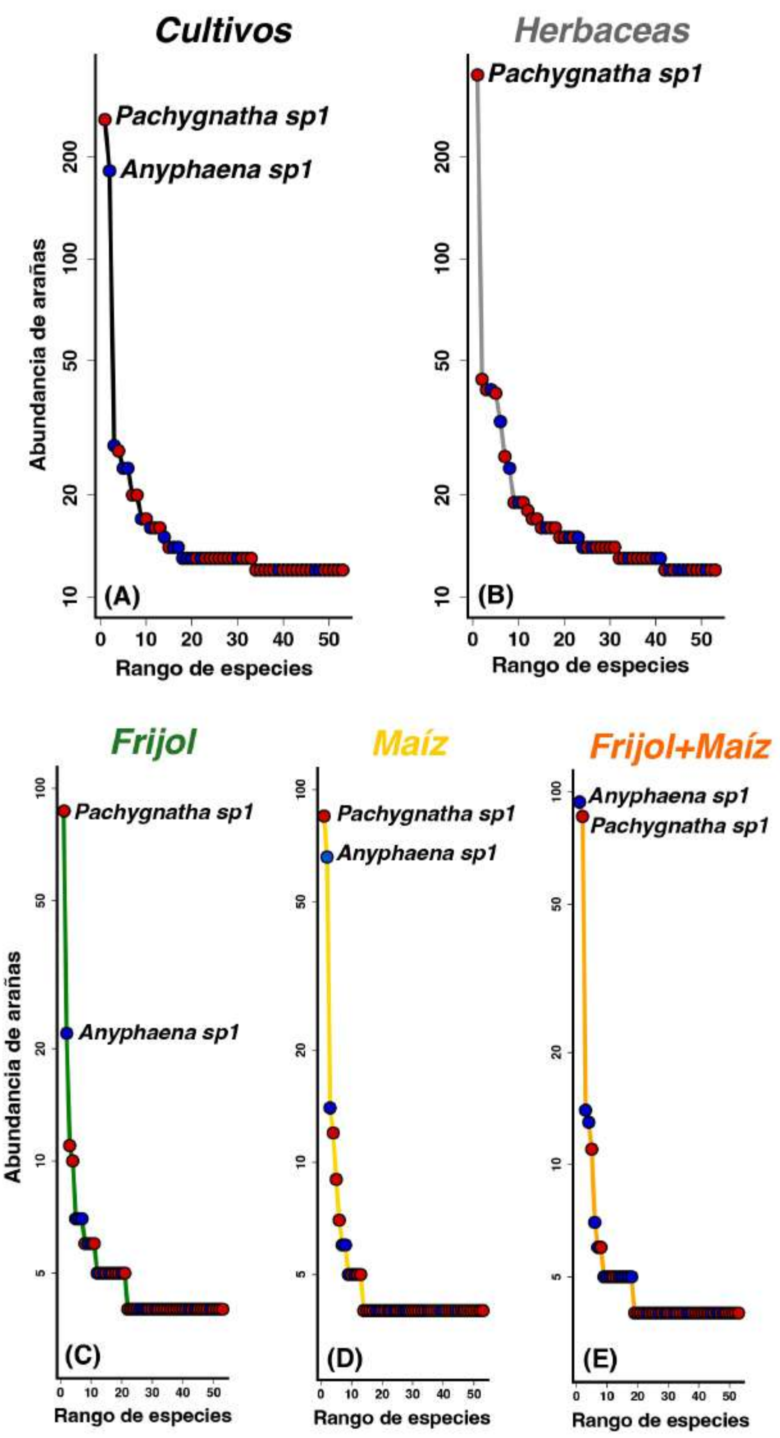

Figura 1. Curvas de rango abundancia de las especies de araña encontradas en los diferentes estratos y tipos de cultivo. Los puntos rojos corresponden con las especies del gremio de

arañas tejedoras, mientras que los puntos azules con especies del gremio de *arañas cazadoras*.

Cuadro 1. Listado de especies y número de arañas de los gremios presentes en los tipos de cultivos y estratos vegetales.

Gremios	**Familias**	**Morfo-Especies**	***Frijol***		***Maíz***		***Frijol + Maíz***	
			Cultivo	**Herbáceas**	**Cultivo**	**Herbáceas**	**Cultivo**	**Herbáceas**
Cazadoras	Anyphaenidae	*Anyphaena* sp1	18	4	62	9	90	8
	Anyphaenidae	*Anyphaena* sp2	3	0	0	3	9	26
	Corinnidae	Corinnidae sp1	0	0	0	1	0	0
	Agelenidae	*Tortonela* sp1	0	0	0	0	1	0
	Agelenidae	*Tortonela* sp2	1	0	0	0	1	0
	Lycosidae	*Pardosa* sp1	2	7	0	2	0	3
	Salticidae	Salticidae sp1	0	1	2	0	10	2
	Salticidae	Salticidae sp2	1	2	2	0	2	0
	Salticidae	Salticidae sp4	0	0	1	0	0	0
	Salticidae	Salticidae sp5	1	0	0	0	0	0
	Thomisidae	*Misumenoides* sp1	3	3	1	0	0	4
	Thomisidae	*Misumenoides* sp2	1	2	0	0	0	0
	Thomisidae	*Misumenoides* sp3	0	0	0	0	0	1
	Thomisidae	*Misumenoides* sp4	2	2	0	0	1	1
	Thomisidae	*Xysticus* sp	0	0	0	0	1	0
	Thomisidae	*Misumenoides* sp5	0	1	0	0	0	0
	Trachelidae	*Trachelas ductonuda*	3	4	10	0	3	0
Tejedoras	Araneidae	Araneidae sp1	0	1	0	0	0	0
	Araneidae	*Neoscona orizabensis*	7	2	0	1	1	0
	Araneidae	*Araneus* sp1	0	0	1	0	0	0
	Araneidae	*Araneus* sp2	0	0	0	2	0	0
	Araneidae	*Araneus* sp3	0	2	0	0	0	3
	Araneidae	*Neoscona* sp1	2	0	0	0	0	0
	Araneidae	*Araneus* sp4	0	0	0	0	0	2
	Araneidae	Araneidae sp7	1	0	0	0	0	0
	Araneidae	*Araneus* sp8	1	2	0	1	0	0
	Araneidae	*Metazigia* sp1	0	0	0	0	1	0
	Linyphiidae	*Erigone* sp1	1	2	0	2	0	3
	Linyphiidae	Linyphiinae sp2	0	0	0	0	1	0

Linyphiidae	Linyphiinae sp3	0	1	0	0	0	0
Linyphiidae	Linyphiinae sp4	0	1	1	0	0	0
Linyphiidae	Linyphiinae sp5	0	0	0	0	0	1
Linyphiidae	Linyphiinae sp6	0	1	0	0	0	1
Linyphiidae	Linyphiinae sp7	0	0	0	2	0	2
Linyphiidae	Linyphiinae sp8	0	1	0	0	0	0
Tetragnathidae	*Pachygnatha* sp1	83	130	81	104	82	104
Tetragnathidae	*Tetragnatha* sp3	6	5	0	0	2	1
Tetragnathidae	Tetragnathidae sp4	2	1	1	14	1	13
Tetragnathidae	Tetragnathidae sp5	0	1	0	0	0	0
Tetragnathidae	Tetragnathidae sp6	1	0	0	0	0	0
Tetragnathidae	*Pachygnatha* sp7	0	0	0	0	0	2
Tetragnathidae	*Pachygnatha* sp7	0	4	0	10	0	15
Tetragnathidae	*Leucauge venusta*	0	1	0	2	1	4
Tetragnathidae	Tetragnathidae sp8	0	0	0	2	0	0
Theridiidae	Theridiidae sp3	1	15	3	15	0	2
Theridiidae	Theridiidae sp1	0	3	8	0	7	11
Theridiidae	Theridiidae sp2	0	0	0	0	0	4
Theridiidae	Theridiidae sp4	0	0	0	4	1	1
Theridiidae	Theridiidae sp5	0	0	5	0	0	0
Theridiidae	Theridiidae sp6	0	0	0	0	0	2
Theridiidae	Theridiidae sp9	0	3	0	1	0	0
Theridiidae	Theridiidae sp8	1	0	0	0	0	1
Theridiidae	Theridiidae sp10	0	2	0	1	0	0
	Total	141	204	178	176	215	217
	Cobertura de muestreo	92.9%	95.1%	97.2%	97.2%	95.3%	96.8%

3.2 Efecto del tipo de cultivo y estrato en la riqueza y abundancia de los gremios de arañas

Encontramos que la abundancia y riqueza de los dos gremios de arañas difirieron entre los diferentes tipos de cultivo y estratos dentro de las parcelas (Cuadro 2, Figura 2 y 3). Las *arañas cazadoras* fueron significativamente más abundantes, pero no presentaron una mayor riqueza de especies en las parcelas con dicultivos, en comparación con los monocultivos de maíz o frijol (Cuadro 2, Figura 2A-B). Los dicultivos tuvieron 190% más abundancia de *arañas cazadoras* que los monocultivos de frijol (32 ind vs 12 ind) y 113% más que los cultivos de maíz (32 ind vs 15 ind, Figura 2A). No encontramos un efecto significativo de la mezcla de cultivos sobre la riqueza o abundancia de las *arañas tejedoras* (Figura 2C-D).

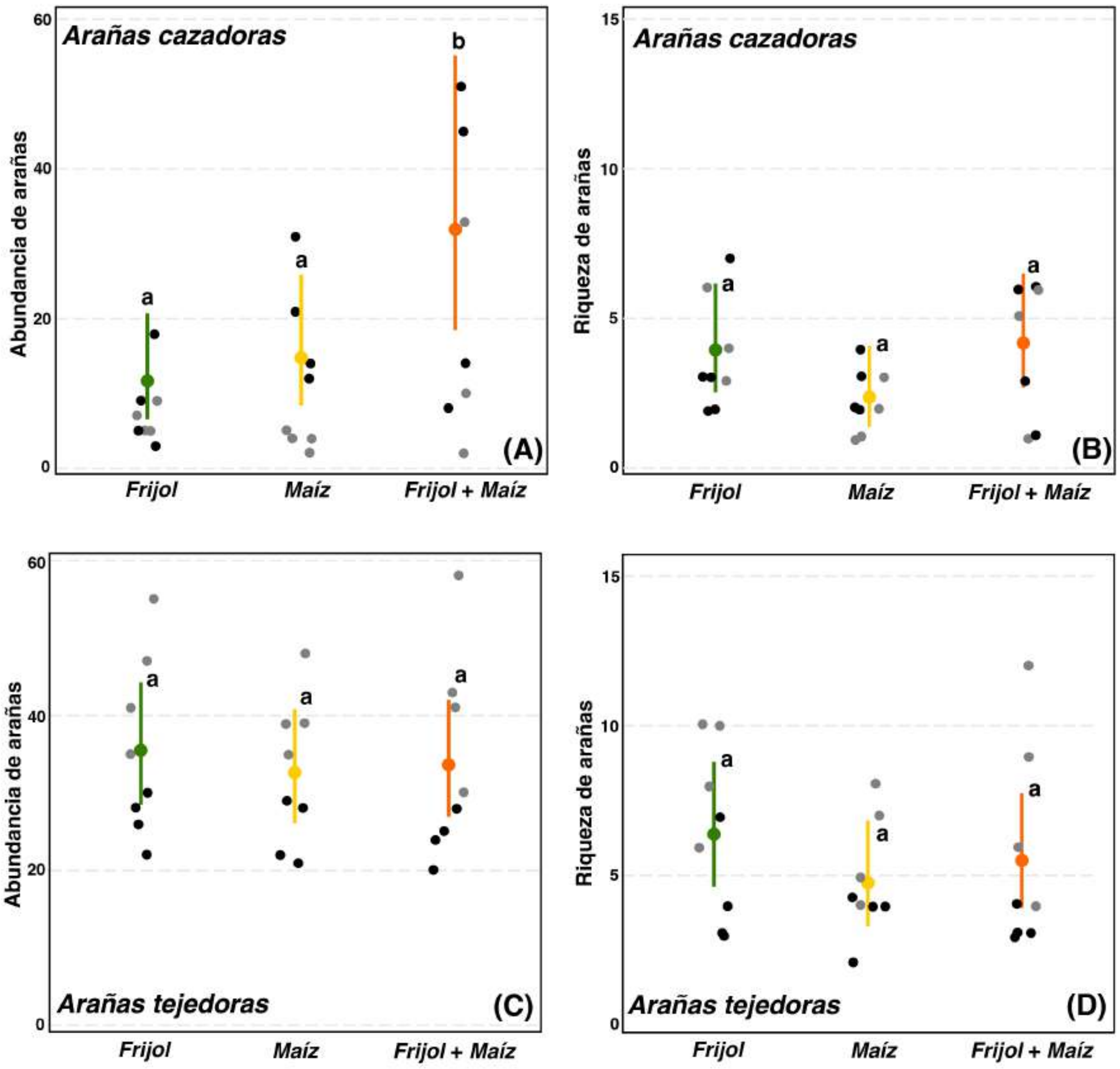

Figura 2. Efecto del tipo de cultivo sobre la abundancia y riqueza de los gremios de *arañas cazadoras* y *tejedoras*. En todos los gráficos el color negro de los puntos corresponde con las

muestras del cultivo y los de color gris con el estrato herbáceo. Letras diferentes encima de las líneas de error (intervalos de confianza) denotan diferencias significativas.

Las *arañas cazadoras* fueron significativamente más abundantes, pero no más ricas en especies en el estrato asociado a las plantas de cultivo (140% más individuos, Figura 3A, Cuadro 2), mientras que las *arañas tejedoras* tuvieron una mayor riqueza (75% más especies) y abundancia (68% más arañas) en el estrato herbáceo que en el cultivo (Figura 3C-D, Cuadro 2).

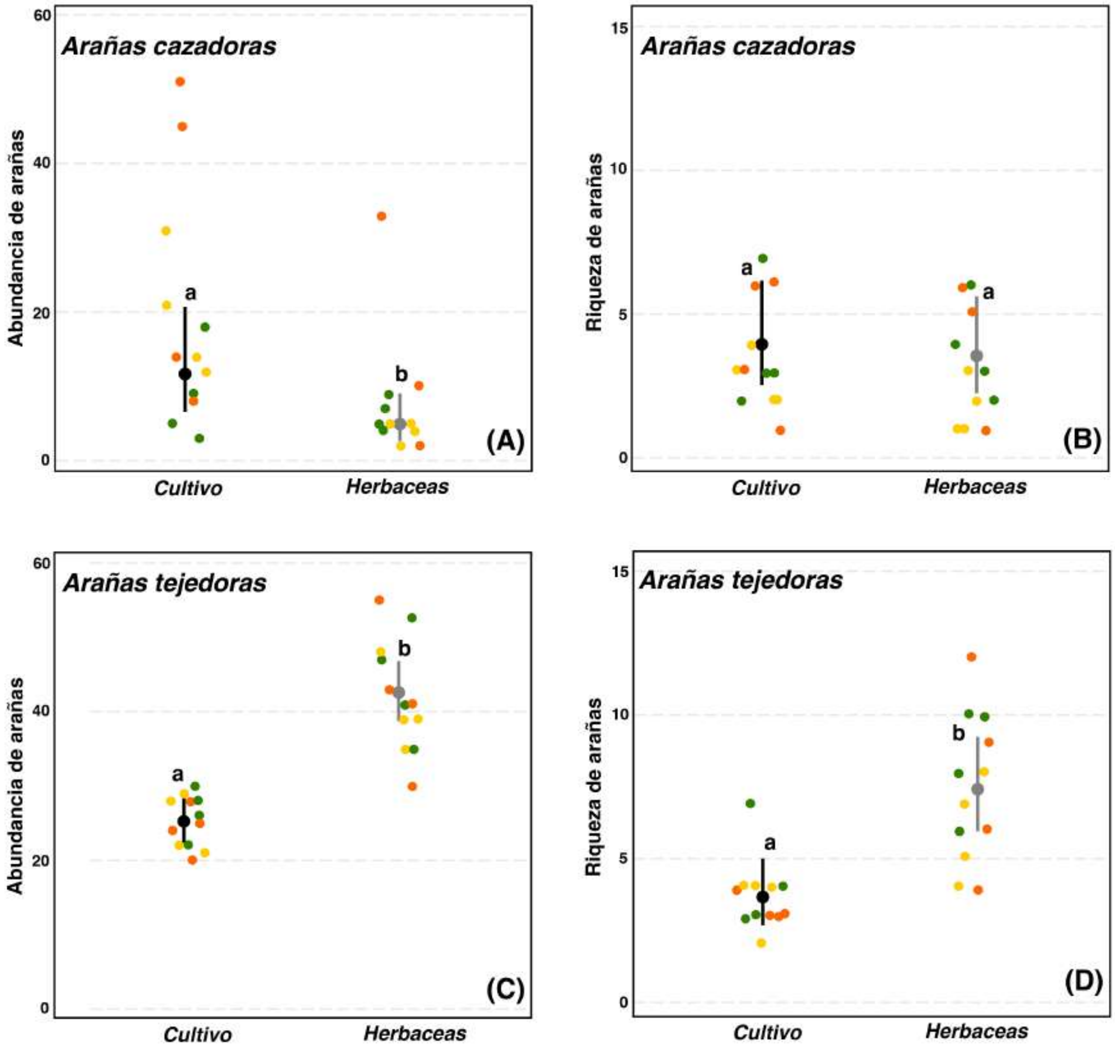

Figura 3. Efecto del estrato vegetal sobre la abundancia y riqueza de los gremios de *arañas cazadoras* y *tejedoras*. En todos los gráficos los puntos de color verde corresponden con muestras de las parcelas sembradas con frijol, los amarillos con parcelas de maíz y los puntos naranjas con parcelas de maíz y frijol. Letras diferentes encima de las líneas de error (intervalos de confianza) denotan diferencias significativas.

Cuadro 2. Resumen de los modelos lineales generalizados (GLM) de la riqueza y abundancia de los gremios de arañas.

Gremios	**Variable dependiente**	**Variables independientes**		**AIC modelo final**	**ΔAIC**
Cazadoras	**Abundancia**	**Tipo de cultivo**	Frijol (11.6 ± 1.21) Maíz (14.7 ± 1.40) Frijol + Maíz (31.9 ± 1.40)	165.2	6.1
		Estratos vegetales	Cultivos (11.6 ± 1.31) Herbáceas (4.9 ± 1.32)		
	Riqueza	**Tipo de cultivo**	ns	na	na
		Estratos vegetales	ns		
Tejedoras	**Abundancia**	**Tipo de cultivo**	ns	157.1	26.1
		Estratos vegetales	Cultivos (25.2 ± 1.06) Herbáceas (42.5 ± 1.07)		
	Riqueza	**Tipo de cultivo**	ns	104.4	12.1
		Estratos vegetales	Cultivos (3.6 ± 1.16) Herbáceas (7.4 ± 1.20)		

Los números entre paréntesis representan los interceptos estimados (promedios) por el modelo y sus errores estándar.

3.3 Diversidad beta de arañas en las diferentes escalas espaciales del cultivo

Observamos para los dos gremios de arañas que la disimilitud en la composición de arañas fue mayor entre los cultivos que entre los estratos vegetales o las unidades de muestreo dentro de las parcelas (Figura 4). Para los dos gremios de arañas, la diversidad beta entre cultivos (β_3) siempre fue mayor que lo esperado por azar. Estos cambios en diversidad beta (β_3) siempre fueron mayores entre los diferentes tipos de cultivos (*e.g.* maíz vs frijol) que entre los mismos tipos de cultivo (frijol vs frijol) (Figura 4). Las *arañas tejedoras* tuvieron un mayor porcentaje de cambio entre los estratos vegetales (β_2), que entre las unidades de muestreo (β_1), a diferencia de las *arañas cazadoras* que tuvieron el patrón contrario (Figura 4).

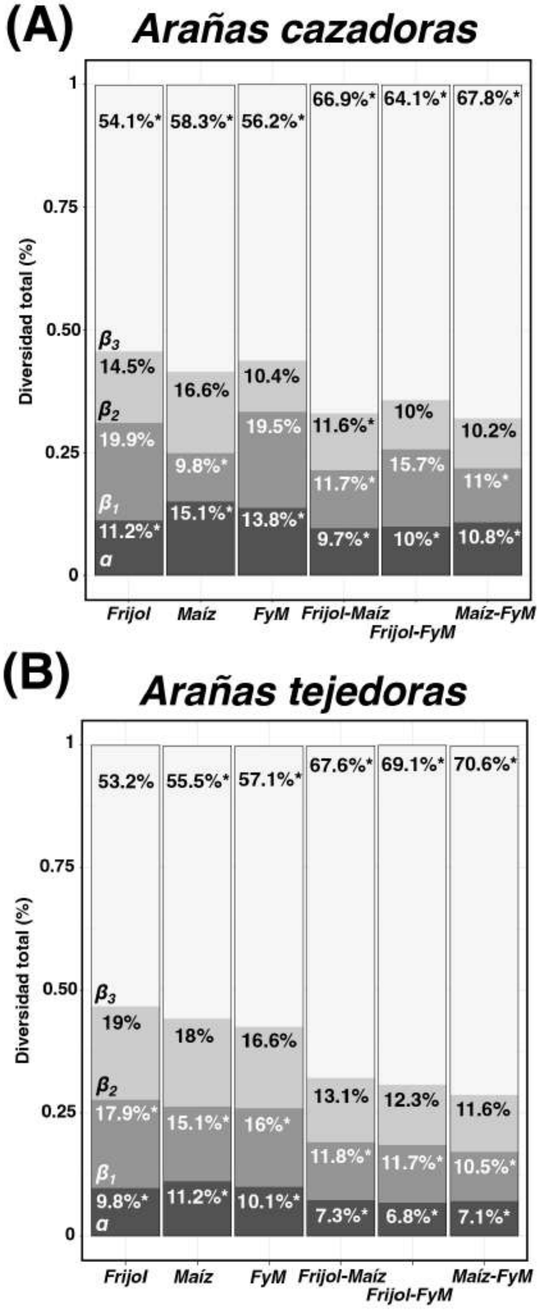

Figura 4. Partición aditiva jerárquica de la diversidad regional de los gremios de arañas (observada vs esperada por azar). (α) diversidad de cada unidad de muestreo, (β_1) diversidad

beta de especies de arañas entre unidades, (β_2) diversidad beta entre estratos dentro de las parcelas, (β_3) diversidad beta entre parcelas de cultivo. Los asteriscos denotan diferencias significativas entre los valores observados y los esperados por azar.

El cambio en composición de especies entre cultivos siempre fue mayor al 50% para los dos gremios de arañas (Cuadro 3). En promedio, las *arañas cazadoras* tuvieron una mayor diversidad beta entre los cultivos (0.72 ± 0.13), que las arañas tejedoras (0.57 ± 0.02). El recambio de especies fue el principal componente de la diversidad beta de *arañas cazadoras* (Recambio= 0.58 ± 0.17, Anidamiento= 0.17 ± 0.1), mientras que los dos componentes tuvieron un aporte similar a los cambios en diversidad beta de las *arañas tejedoras* entre los cultivos (Recambio= 0.28 ± 0.03, Anidamiento= 0.28 ± 0.009) (Cuadro 3).

Cuadro 3. Diversidad beta total, recambio y anidamiento de los diferentes gremios de arañas dentro y entre los diferentes tipos de cultivos.

Gremio	**Cultivos**	**Diversidad beta**		
		Total	**Recambio**	**Anidamiento**
Arañas cazadoras	*Frijol*	0.875	0.806	0.069
	Maíz	0.503	0.306	0.196
	Frijol+Maíz	0.747	0.591	0.156
	Frijol vs Maíz	0.822	0.718	0.104
	Frijol vs Frijol+Maíz	0.645	0.473	0.173
	Maíz vs Frijol+Maíz	0.738	0.626	0.112
Arañas tejedoras	*Frijol*	0.61	0.332	0.277
	Maíz	0.547	0.252	0.294
	Frijol+Maíz	0.568	0.265	0.303
	Frijol vs Maíz	0.596	0.31	0.286
	Frijol vs Frijol+Maíz	0.56	0.266	0.294
	Maíz vs Frijol+Maíz	0.585	0.3	0.284

4. Discusión

La diversificación vegetal interespecífica en uno o varios estratos vegetales se ha propuesto como una práctica agroecológica que propicia la presencia de depredadores como las arañas en los cultivos (Lichtenberg et al., 2017; Sunderland y Samu, 2000), lo cual puede favorecer su rendimiento productivo y económico, debido al control efectivo de las plagas (Michalko et al., 2019). Sin embargo, dadas las diferencias en estrategias de caza y grado de asociación variable con las plantas (Cardoso et al., 2011, Vasconcellos-Neto et al. 2017), es probable que los gremios de arañas respondan y se ensamblen de diferente manera en cultivos diversificados en uno o varios estratos (Sunderland and Samu, 2000). En el presente estudio, encontramos que la mezcla de leguminosas con plantas de maíz en forma de dicultivo propiciaba comunidades de *arañas cazadoras* más abundantes en comparación con monocultivos de maíz o frijol, lo cual podría mejorar el rendimiento de los cultivos mixtos. También, encontramos que la riqueza y abundancia de arañas difería entre los estratos dentro los cultivos (*herbáceas no cultivadas* vs *plantas del cultivo*), sin embargo, la respuesta de las especies dependía del gremio trófico. Por último, encontramos que la diversidad regional de arañas de ambos gremios estuvo mayormente explicada por una alta diversidad beta entre los tipos de cultivos.

Se sabe que pocas especies dominantes de arañas y otros depredadores son las encargadas de llevar a cabo la mayor parte del control natural de las poblaciones de herbívoros, entre ellos las plagas de los cultivos (Lichtenberg et al., 2017). En este estudio, encontramos que la comunidad de arañas en los cultivos y estratos vegetales estuvo dominada por dos especies (68% de la abundancia total), una del género *Pachygnatha* perteneciente al gremio de las *tejedoras* (51%) y una araña *cazadora* de la vegetación del género *Anyphaena*

(17%). La dominancia de pocas especies de arañas es un patrón común en los cultivos de cereal como el maíz (Farinós et al., 2008; Santiago-Pacheco et al., 2017) y en otros sistemas agrícolas del mundo (Birkhofer et al., 2013; Nyffeler y Sunderland, 2003). La dominancia de dos especies pertenecientes a gremios tróficos diferentes, puede estar indicando un patrón de control biológico complementario (Lichtenberg et al., 2017) por parte de las arañas en el sistema agrícola que estudiamos. Se ha demostrado que las arañas como *Pachygnatha* y otras *tejedoras* son más propensas a capturar insectos como moscas o áfidos, mientras que las *arañas cazadoras* como *Anyphaena* tienen una dieta más variada que incluye especies de lepidópteros y hemípteros, taxones a los que pertenecen las principales plagas del maíz (Blanco et al., 2014; Nyffeler y Sunderland, 2003). Dentro de nuestra escala de estudio, encontramos que el establecer dicultivos de maíz y frijol provoca un cambio en la dominancia de las arañas, favoreciéndose la especie de *Anyphaena* la cual se torna igual o mayormente numerosa que la especie de *Pachygnatha*. Dado que las *arañas cazadoras* tienen el potencial de depredar especies pertenecientes a taxones que atacan con mayor probabilidad el maíz (Nyffeler y Sunderland, 2003), mantener estos cultivos en su forma tradicional de siembra con leguminosas y otras especies adicionadas (*milpa*), podría ser una práctica útil para mejorar el control de plagas (Lichtenberg et al., 2017; Poveda et al., 2008).

Demostramos que la mezcla de leguminosas con plantas de maíz en forma de dicultivo provocó una mayor abundancia de *arañas cazadoras* en un 113% con respecto a los monocultivos de maíz (32 Ind. vs 15 Ind.) y del 190% en comparación con los monocultivos de frijol (32 Ind. vs 11 Ind.), en este sentido el efecto de la mezcla de cultivos sobre la abundancia promedio de arañas, resultó ser sinérgico (*i.e.* mayor a la suma de la abundancia de los monocultivos, 26 Ind.) y no aditivo o negativo (Sunderland y Samu, 2000). Las arañas del gremio de *cazadoras* fueron más comunes en las plantas principales del cultivo

(Armendano y González, 2011) y se ha demostrado que estas especies tienen algún grado de asociación con la vegetación, incluyendo los cultivos (Vasconcellos-Neto et al. 2017), por lo tanto es de esperarse que la adición de nuevos refugios, un mejor clima y más presas, propiciado por la mezcla de plantas leguminosas con el maíz, haya provocado una diferencia significativa en su abundancia en comparación con las *arañas tejedoras* (Poveda et al., 2008, Vasconcellos-Neto et al. 2017). Al igual que en otros estudios (Beaumelle et al., 2021; Quijano et al., *en rev*; Rusch et al., 2014), demostramos que solo la abundancia de arañas y no la riqueza de especies, responde positivamente al manejo local de las parcelas, incluso de un gremio como las *cazadoras* con gran ocurrencia en las plantas del cultivo manejadas. Consideramos que la diversificación con plantas estructuralmente complementarias (leguminosas y maíz) crea nuevos hábitats para diversas especies (Poveda et al., 2008), pero es probable que estos nuevos sitios y presas sean mayoritariamente ocupados por las arañas dominantes (*Anyphaena* sp) las cuales desplazan a las especies menos generalistas.

Las arañas *tejedoras* no respondieron significativamente al manejo de las parcelas a través de la mezcla de cultivos, pero como esperábamos, las arañas de este gremio fueron más diversas en el estrato herbáceo no cultivado que en las plantas principales del cultivo (Benamú et al., 2017). Previamente se ha reportado que, en algunos cultivos de cereal como la soya, las familias de arañas *tejedoras* como Tetragnathidae, Araneidae o Theridiidae son más comunes en las plantas herbáceas que crecen libremente dentro o alrededor de los cultivos (Benamú et al., 2017). Esta mayor dominancia del gremio de *tejedoras* en las herbáceas no cultivadas (Benamú et al., 2017), sugiere que este estrato alberga gran proporción de las arañas que potencialmente pueden colonizar las plantas principales del cultivo (Amaral et al., 2016; Schmidt-Entling y Döbeli, 2009), por lo tanto, es deseable propiciar un manejo diferente al tradicionalmente extractivo (Altieri y Nicholls, 2004;

Penagos et al., 2003) para fomentar sus poblaciones. Adicionalmente, aunque las *arañas cazadoras* no fueron más comunes en las plantas herbáceas, parte de la diversidad de especies de este gremio es mantenida en este estrato (≈30% de la abundancia total), lo cual resalta la importancia de estas plantas silvestres para la diversidad de arañas que habitan la vegetación (Amaral et al., 2016).

Tal como habíamos predicho, encontramos que la diversidad regional de ambos gremios se debía en mayor proporción a los cambios en la composición de arañas entre tipos de cultivo (monocultivos y dicultivos), que entre estratos vegetales o unidades de muestreo dentro de las parcelas de cultivo. No encontramos que los cambios en diversidad beta entre parcelas sembradas con maíz o frijol fueran mucho más altos que los cambios en composición de especies entre parcelas con el mismo cultivo (monocultivos), o parcelas con ambos tipos de cultivo. Este resultado indica que independientemente del tipo de cultivo, solo el hecho de mezclar los cultivos en el paisaje puede potenciar la diversidad regional de arañas al propiciar ensambles de arañas diferentes, lo cual ya se había sugerido anteriormente (Ouyang et al., 2020; Redlich et al., 2018; Rusch et al., 2013; Wezel et al., 2014). En este caso, es probable que las diferencias en composición de arañas se deban a filtros relacionados con los cambios en estructura vegetal entre los cultivos (Stuntz et al., 2002b). Consideramos que la variación en el tipo y densidad de las hojas y tallos de las plantas de los diferentes cultivos (*e.g.* maíz vs frijol) o la variación en el tipo de presas que estos albergan (Greenstone, 1984; Rypstra et al., 1999), haya causado que las especies de los diferentes gremios se recambien más entre los cultivos que lo esperado por azar. Este recambio de especies (*sensu* Baselga, 2010) fue mayor para las arañas que cazan activamente en la vegetación (*cazadoras* = 0.58 ± 0.17 vs *tejedoras* = 0.28 ± 0.03), y es probable que esto también se deba al alto grado de especificidad que tienen algunas *arañas cazadoras* por la vegetación, incluyendo la de los cultivos (Vasconcellos-Neto et al. 2017). Una mayor diversidad regional de arañas debido a la mezcla de cultivos tiene el potencial de contribuir a un consumo efectivo de una amplia gama de insectos herbívoros entre ellos algunas especies de plagas que reducen la producción de los cultivos (Birkhofer et al., 2013; Wezel et al., 2014).

5. Conclusiones y recomendaciones

Nuestro estudio ofrece nueva evidencia empírica y experimental que apoya la ventaja de tener diferentes cultivos mezclados (dicultivos) con el fin de propiciar comunidades de arañas más diversas (por lo menos más abundantes) que en los monocultivos. Esta mezcla de diferentes cultivos y estratos vegetales, tiene la ventaja de crear ensambles locales y regionales diversos que pueden tener un mejor aporte al control de herbívoros, lo cual crea efectos de arriba hacia abajo que en la mayoría de casos aumenta el rendimiento de los cultivos, entre ellos los cultivos de cereal (Michalko et al., 2019). Nuestros hallazgos sugieren que los gremios de arañas con estrategias de caza y grado de dominancia diferente (Uetz et al., 1999), y además asociación variable con la vegetación (Vasconcellos-Neto et al. 2017), responden de manera diferencial a la modificación local de los cultivos. Por lo tanto, para potenciar una alta diversidad funcional de arañas se debe manejar la estructura vegetal de los cultivos en varios estratos. Es recomendable en futuras investigaciones analizar el efecto que tienen las prácticas agroecológicas como la diversificación vegetal sobre las interacciones de depredación de las arañas y su papel en el control biológico de las especies de plagas con ocurrencia en los diferentes estratos vegetales y cultivos.

6. Bibliografía

Altieri, M., Nicholls, C., 2004. Biodiversity and Pest Management in Agroecosystems, Second. ed, Food Products Press.

Altieri, M.A., Trujillo, J., 1987. The agroecology of corn production in Tlaxcala, Mexico. Hum. Ecol. 15, 189–220. https://doi.org/10.1007/BF00888380

Amaral, D.S.S.L., Venzon, M., dos Santos, H.H., Sujii, E.R., Schmidt, J.M., Harwood, J.D., 2016. Non-crop plant communities conserve spider populations in chili pepper agroecosystems. Biol. Control 103, 69–77. https://doi.org/10.1016/j.biocontrol.2016.07.007

Antoniazzi, R., Guevara, R., García-Franco, J., Janda, M., Leponce, M., Dáttilo, W., 2020. Environmental drivers of ant dominance in a tropical rainforest canopy at different spatial scales. Ecol. Entomol. https://doi.org/10.1111/een.12988

Armendano, A., González, A., 2011. Spider fauna associated with wheat crops and adjacent habitats in Buenos Aires, Argentina. Rev. Mex. Biodivers. 82, 1176–1182. https://doi.org/10.22201/ib.20078706e.2011.4.734

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga A, Orme D, Villeger S, De Bortoli J, Leprieur F, Logez M (2022). betapart: Partitioning Beta Diversity into Turnover and Nestedness Components_. R package version 1.5.6. https://CRAN.R-project.org/package=betapart

Bartoń K., 2022. MuMIn: Multi-Model Inference. R package version 1.47.1. https://CRAN.R-project.org/package=MuMIn

Beaumelle, L., Auriol, A., Grasset, M., Pavy, A., Thiéry, D., Rusch, A., 2021. Benefits of increased cover crop diversity for predators and biological pest control depend on the landscape context. Ecol. Solut. Evid. 2, 1–12. https://doi.org/10.1002/2688-8319.12086

Benamú, M.A., Lacava, M., García, L.F., Santana, M., Viera, C., 2017. Spiders associated with agroecosystems: Roles and perspectives, in: Behaviour and Ecology of Spiders: Contributions from the Neotropical Region. Springer International Publishing, pp. 275–302. https://doi.org/10.1007/978-3-319-65717-2_11

Bianchi, F.J.J.A., Booij, C.J.H., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: A review on landscape composition, biodiversity and natural pest control. Proc. R. Soc. B Biol. Sci. 273, 1715–1727. https://doi.org/10.1098/rspb.2006.3530

Birkhofer, K., Entling, M.H., Lubin, Y., 2013. Agroecology: Trait composition, spatial relationships, trophic interactions, in: Penney, D. (Ed.), Spider Research in the 21st Century Trends & Perspectives. Siri Scientific Press, Manchester, pp. 200–229. https://doi.org/10.1007/978-0-387-76495-5

Blanco, C.A., Pellegaud, J.G., Nava-Camberos, U., Lugo-Barrera, D., Vega-Aquino, P., Coello, J., Terán-Vargas, A.P., Vargas-Camplis, J., 2014. Maize pests in Mexico and challenges for the adoption of integrated pest management programs. J. Integr. Pest Manag. 5. https://doi.org/10.1603/IPM14006

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference 2nd ed., Berlin: Springer.

Cardoso, P., Pekár, S., Jocqué, R., Coddington, J.A., 2011. Global patterns of guild composition and functional diversity of spiders. PLoS One 6, 1–10. https://doi.org/10.1371/journal.pone.0021710

Coll, M., Bottrell, D., 1995. Predator-prey association in mono- and dicultures: Effect of maize and bean vegetation. Agric. Ecosyst. Environ. 54, 115–125.

Crist, T.O., Veech, J.A., Gering, J.C., Summerville, K.S., 2003. Partitioning Species Diversity across Landscapes and Regions: A Hierarchical Analysis of α, β, and γ Diversity. Am. Nat. 162, 734–743. https://doi.org/10.1086/378901

Escobar-Ramírez, S., Tscharntke, T., Armbrecht, I., Torres, W., 2020. Grass, IngoDecrease in β-diversity, but not in α-diversity, of ants in intensively managed coffee plantations. Insect Conservation and Diversity. 13, 445-455. 10.1111/icad.12417

FAO. [FAOSTAT, Land Cover]. License: CC BY-NC-SA 3.0 IGO. Extracted from: [https://www.fao.org/faostat/en/#data/LC]. Data of Access: [01-06-2023]

Farinós, G.P., de la Poza, M., Hernández-Crespo, P., Ortego, F., Castañera, P., 2008. Diversity and seasonal phenology of aboveground arthropods in conventional and transgenic maize crops in Central Spain. Biol. Control 44, 362–371. https://doi.org/10.1016/j.biocontrol.2007.11.007

Gering, J.C., Crist, T.O., Veech, J.A., 2003. Additive partitioning of species diversity across multiple spatial scales: Implications for regional conservation of biodiversity. Conserv. Biol. 17, 488–499. https://doi.org/10.1046/j.1523-1739.2003.01465.x

Gliessman, S.R., 2015. Agroecology The Ecology of Sustainable Food Systems.

Greenstone, M.H., 1984. Determinants of web spider species diversity: Vegetation structural diversity vs. prey availability. Oecologia 62, 299–304. https://doi.org/10.1007/BF00384260

Jost, L., Devries, P., Walla, T., Greeney, H., Chao, A., Ricotta, C., 2010. Partitioning diversity for conservation analyses. Divers. Distrib. 16, 65–76. https://doi.org/10.1111/j.1472-4642.2009.00626.x

Letourneau, D.K., 1990. Mechanisms of predator accumulation in a mixed crop system. Ecol. Entomol. 15, 63–69. https://doi.org/10.1111/j.1365-2311.1990.tb00784.x

Letourneau, D.K., Jedlicka, J.A., Bothwell, S.G., Moreno, C.R., 2009. Effects of Natural Enemy Biodiversity on the Suppression of Arthropod Herbivores in Terrestrial Ecosystems. Annu. Rev. Ecol. Evol. Syst. 40, 573–592. https://doi.org/10.1146/annurev.ecolsys.110308.120320

Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., Bosque-Pérez, N.A., Carvalheiro, L.G., Snyder, W.E., Williams, N.M., Winfree, R., Klatt, B.K., Åström, S., Benjamin, F., Brittain, C., Chaplin-Kramer, R., Clough, Y., Danforth, B., Diekötter, T., Eigenbrode, S.D., Ekroos, J., Elle, E., Freitas, B.M., Fukuda, Y., Gaines-Day, H.R., Grab, H., Gratton, C., Holzschuh, A., Isaacs, R., Isaia, M., Jha, S., Jonason, D., Jones, V.P., Klein, A.M., Krauss, J., Letourneau, D.K., Macfadyen, S., Mallinger, R.E., Martin, E.A., Martinez, E., Memmott, J., Morandin, L., Neame, L., Otieno, M., Park, M.G., Pfiffner, L., Pocock, M.J.O., Ponce, C., Potts, S.G., Poveda, K., Ramos, M., Rosenheim, J.A., Rundlöf, M., Sardiñas, H., Saunders, M.E., Schon, N.L., Sciligo, A.R., Sidhu, C.S., Steffan-Dewenter, I., Tscharntke, T., Veselý, M., Weisser, W.W., Wilson, J.K., Crowder, D.W., 2017. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. Glob. Chang. Biol. 23, 4946–4957. https://doi.org/10.1111/gcb.13714

Martínez-Camacho, Y.D., Negrete-Yankelevich, S., Maldonado-Mendoza, I.E., Núñez-de la Mora, A., Amescua-Villela, G., 2022. Agroecological management with intra- and interspecific diversification as an alternative to conventional soil nutrient management in family maize farming. Agroecol. Sustain. Food Syst. 46, 364–391. https://doi.org/10.1080/21683565.2021.2015736

Michalko, R., Birkhofer, K., Pekár, S., 2021. Interaction between hunting strategy, habitat type and stratum drive intraguild predation and cannibalism. Oikos 1–12. https://doi.org/10.1111/oik.08355

Michalko, R., Pekár, S., Dul, M., 2019. Global patterns in the biocontrol efficacy of spiders: A meta - analysis 1366–1378. https://doi.org/10.1111/geb.12927

Nyffeler, M., Sunderland, K.D., 2003. Composition, abundance and pest control potential of spider communities in agroecosystems: A comparison of European and US studies. Agric. Ecosyst. Environ. 95, 579–612. https://doi.org/10.1016/S0167-8809(02)00181-0

Ouyang, F., Su, W., Zhang, Y., Liu, X., Su, J., Zhang, Q., Men, X., Ju, Q., Ge, F., 2020. Ecological control service of the predatory natural enemy and its maintaining mechanism in rotation-intercropping ecosystem via wheat-maize-cotton. Agric. Ecosyst. Environ. 301, 107024. https://doi.org/10.1016/j.agee.2020.107024

Oksanen, J., Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P., O'Hara, R.B., Simpson, G., Solymos, P., Stevens, M., Szoecs, E. & Wagner, H. 2020). vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project. org/package=vegan

Paredes, D., Rosenheim, J.A., Chaplin-Kramer, R., Winter, S., Karp, D.S., 2021. Landscape simplification increases vineyard pest outbreaks and insecticide use. Ecol. Lett. 24, 73–83. https://doi.org/10.1111/ele.13622

Penagos, D.I., Magallanes, R., Valle, J., Cisneros, J., Martínez, A.M., Goulson, D., Chapman, J.W., Caballero, P., Cave, R.D., Williams, T., 2003. Effect of weeds on insect pests of maize and their natural enemies in Southern Mexico. Int. J. Pest Manag. 49, 155–161. https://doi.org/10.1080/0967087021000043111

Poveda, K., Gómez, M.I., Martínez, E., 2008. Diversification practices: Their effect on pest regulation and production. Rev. Colomb. Entomol. 34, 131–144.

R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Quijano-Cuervo, L., del-Val, E., Macías-Ordóñez, R., Dátillo, W., Negrete-Yankelevich, S. (*en revisión*) Spider Guilds in a Maize Polyculture Respond Differently to Crop Diversification, Landscape Composition and Stage of the Agricultural Cycle. Available at SSRN: https://ssrn.com/abstract=4462390 or http://dx.doi.org/10.2139/ssrn.4462390

Redlich, S., Martin, E.A., Steffan-Dewenter, I., 2018. Landscape-level crop diversity benefits biological pest control. J. Appl. Ecol. 55, 2419–2428. https://doi.org/10.1111/1365-2664.13126

Riechert, S., Bishop, L., 1990. Prey Control by an Assemblage of Generalist Predators : Spiders in Garden Test Systems. Ecology 71, 1441–1450.

Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G., Ekbom, B., 2014. Management intensity at field and landscape levels affects the structure of generalist predator communities. Oecologia 175, 971–983. https://doi.org/10.1007/s00442-014-2949-z

Rusch, A., Bommarco, R., Jonsson, M., Smith, H.G., Ekbom, B., 2013. Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale. J. Appl. Ecol. 50, 345–354. https://doi.org/10.1111/1365-2664.12055

Rypstra, A.L., Carter, P.E., Balfour, R.A., Marshall, S.D., 1999. Architectural features of agricultural habitats and their impact on the spider inhabitants. J. Arachnol. 27, 371–377. https://doi.org/10.2307/3706009

Samu, F., Sunderland, K.D., Szinetar, C., 1999. Scale-dependent dispersal and distribution patterns of spidersin agricultural systems: A review. J. Arachnol. 27, 325–332. https://doi.org/10.2307/3706004

Santiago-Pacheco, G., Ángel García-García, M., Martínez-Martínez, L., 2017. Diversidad de arañas (Chelicerata: Araneae) en cultivos de maíz en San Andrés Huayapam, Oaxaca, México. Entomol. Mex. 4, 15–20.

Schmidt-Entling, M.H., Döbeli, J., 2009. Sown wildflower areas to enhance spiders in arable fields. Agric. Ecosyst. Environ. 133, 19–22. https://doi.org/10.1016/j.agee.2009.04.015

Stuntz, S., Simon, U., Zotz, G., 1999. Assessing the potential influence of vascular epiphytes on arthropod diversity in tropical tree crowns: hypothesis, approaches, and preliminary data. Selbyana 20, 276–283. https://doi.org/10.2307/41760033

Stuntz, S., Ziegler, C., Simon, U., Zotz, G., 2002. Diversity and structure of the arthropod fauna within three canopy epiphyte species in central Panama. J. Trop. Ecol. 18, 161–176. https://doi.org/10.1017/S0266467402002110

Sunderland, K., Samu, F., 2000. Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: A review. Entomol. Exp. Appl. https://doi.org/10.1023/A:1003986225443

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31, 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T., Kleijn, D., Rand, T., Tylianakis, J., Nouhuys, S., Vidal, S., 2007. Conservation biological control and enemy diversity on a landscape scale. Biological Control. 43, 294-309. 10.1016/j.biocontrol.2007.08.006

Ubick, D., Paquin, P., Cushing, P.E., Roth, V., 2005. Spiders of North America: an identification manual. Second ed. American Arachnological Society.

Uetz, G.W., Halaj, J., Cady, A.B., 1999. Guild structure of spider in major crops. J. Arachnol. 27, 270–280.

Vasconcellos-Neto, J., Fanchini, Y., da Silva, H., Villanueva-Bonila, G., Romero, G., 2017. Spider–Plant Interactions: An Ecological Approach. En: Viera, C., Gonzaga, M. (eds). Behaviour and Ecology of Spiders. Springer.

Wezel, A., Casagrande, M., Celette, F., Vian, J.F., Ferrer, A., Peigné, J., 2014. Agroecological practices for sustainable agriculture. A review. Agron. Sustain. Dev. 34, 1–20. https://doi.org/10.1007/s13593-013-0180-7

World Spider Catalog. 2023. World Spider Catalog. Version 24. Natural History Museum Bern. http://wsc.nmbe.ch